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THE GENITAL SYSTEM AND THE FETAL MEMBRANES AS CRITERIA FOR MAMMALIAN PHYLOGENY AND TAXONOMY

BY H. W. MOSSMAN

All systems of classification of natural phenomena are admittedly imperfect because these phenomena differ from one another in such infinitely variable degrees that it is impossible to divide them into a system of groupings which do not frequently overlap or intergrade. It is also absolutely impossible consistently to select morphological criteria for a scheme of classification that will lend themselves to the assignment of a series of ranks such as species, genera, and families, in one group that will be of parallel value to a similar series assigned to another related group. Yet in spite of these obviously insurmountable barriers to perfection, convenience and orderliness in science demand that classifications be made, and that their categories be of as nearly parallel value as possible.

Most biologists believe that the best basis for classification is phylogeny, that is, the evolutionary or genetic relationships within and of the group. This is so widely accepted that practically all other forms of classification are considered "artificial." Although artificial classification is often temporarily necessary, as in tentatively fitting a poorly understood entity into a general scheme, still a natural or phylogenetic classification should always be the ultimate aim.

Criteria for classification of any group should therefore be characters of phylogenetic significance. Furthermore there should be some way to evaluate the relative significance of one set of criteria in relation to another set; for instance, dentition as compared to skull proportions; or pelage as compared to baculum. There should also be some method for determining whether a given set of characters is suitable for separating the lower categories such as species and genera, or the higher categories such as families and orders.

The more conservative characters obviously will be of greater value in characterizing the higher categories, while the less conservative will only be of use in the lower categories. The presence of the fetal membranes (amnion, chorion, yolk sac, and allantois) is a highly conservative character appearing in all Amniota. Yet certain aspects of the finer morphology of the placenta, such as whether it is villous, trabecular, or labyrinthine, are of use only in characterizing the families within a suborder, for example the Anthropoidea. This is true be-

cause parallel transitions in placental morphology are known to occur independently in other orders not closely related to the Anthropoidea or to one another. These same aspects of finer morphology are, however, too conservative to be of much use in separating genera or species, there being very slight or no differences in this character within single families or genera.

The relative conservatism of biological characters is based on two entirely distinct and independent things. The first is the human factor, or simply the question of generality versus particularity of concept. The greater the breadth or inclusiveness of a character concept the more conservative it is within its particular field. For example, the character "bony skeleton" is much broader and therefore much more conservative than the character "cranium", while the latter is in turn much broader and more conservative than "zygoma." We can and do quite properly select the generalized and broader characters as criteria for separating the higher categories, and the more narrow and particular ones for the lower subdivisions.

Superimposed on this, much more complex, and equally as important, is the second or biological factor in determining conservatism. This may be expressed as the degree to which a character has been subjected to natural selection.

Assuming equal, intrinsic genetic factors, it is certainly true that the more intimately a character is related to the environment the more rapid and extensive will be its environmental adaptations during the course of evolution. The main thesis of this discussion rests on this assumption. It is maintained that the structural characters of the reproductive tracts and fetal membranes of mammals, because they have been largely independent of environmental selection, show relatively little evolutionary divergence as compared to most other organ systems. This is not the place to discuss, statistically, results to be expected in the evolution of a genetically variable system subjected to environmental selection in contrast to one subjected to very little and indirect environmental action. However, it can be readily understood that without the selective effects of *differing environments*, variations would tend to be submerged because of continuous selection for *one constant set of environmental conditions*. A race under these conditions would become more and more stabilized and specialized, but no new divergent races would arise from it. But this is not the situation in regard to a genetically variable system, such as the fetal membranes that are practically *isolated from any direct selective effects of external environment*. In such a system, in this case the fetal membranes, evolution is free to proceed along almost any line so long as it meets certain vital requirements: (1) the supplying of a means of maintaining an embryo within the mother's uterus until mature enough to be born; (2) structural conditions which will allow the uterus to resume a normal nonpregnant state after delivery, so that another pregnancy may ensue.

Certainly these fundamental requirements are far from simple in either a structural or physiological sense; they involve extremely complex mechanisms. But the point is that not only is the intrauterine environment relatively constant in mammals generally, but so are the requirements for maintenance of an

embryo and for restorability of the uterus to the condition for beginning another pregnancy.

What then should one expect of the evolution of an organ system, such as the fetal membranes, largely isolated from the external environment and charged with a highly complex job to do, but one which is fundamentally the same in all members of the group, in this case the Subclass Eutheria? It seems that, regardless of rate of genetic variation of the system, divergence would be relatively slow and narrow, and that intergradation would be the rule, there being slight environmental selection, and little race isolation due directly to adaptive variations in this system itself. But while this type of evolution would be taking place in an environmentally independent organ system, the group of organisms in which the organ system existed could nevertheless be undergoing the usual evolutionary course in its other organ systems: diverging widely in adaptation to environmental niches old or new; losing species or whole major groups by extinction; in short, becoming the widely divergent, often aberrant or isolated groups that are characteristic of mammals at the present time.

Such an environmentally isolated system must then be very conservative in its characters as compared to those organ systems related closely to the environment and therefore subject to intense, adaptive evolution. The characteristics of such a system should vary relatively little between major groups, and almost none between closely related minor categories. This lack of divergence should make it possible to detect common characteristics among groups widely separated from one another in other characteristics, whether this be due to adaptations to divergent environments, or to extinction of intergrading groups. Conversely, dissimilarity in characters of a conservative organ system should be good evidence of lack of close phylogenetic relationship.

It is generally conceded that similarity of more conservative characters between two forms is better evidence of close relationship than similarity of less conservative characters. Whether lack of conservatism is due to more intensive environmental selection or to a combination of this with such things as more intensive sexual selection, or greater innate potential of genetic variability, there is more chance that similarities in less conservative characteristics are due to evolutionary parallelism or convergence. In estimating phylogenetic relationship it is therefore extremely important to know which are the more conservative organ systems and to give their characters the greater weight. It is also important to evaluate the various characters of such an organ system to determine which are the more conservative within the system. The more conservative will serve to characterize the higher categories, the less only the lower ones.

The foregoing discussion largely reiterates generally recognized principles which have been used for years by students of evolution and taxonomy. However it seemed best to restate them here since the chief purpose of this paper is to point out that the reproductive tracts and fetal membranes of mammals are conservative systems which have never been adequately used in phylogenetic and taxonomic studies of this group. It will be shown that the relative conservatism of the various features of these organ systems can be estimated and the

characters used as criteria in proper relation to their significance. It is now best to proceed to specific examples. The first concerns the male genital tract of the Sciuridae.

In 1923, Pocock pointed out the marked difference between the male external genitalia of *Tamiasciurus* and *Sciurus* and separated the two genera on this basis. In 1932, Mossman, Lawlah, and Bradley published a more detailed study of the tracts of *Sciurus carolinensis*, *S. niger*, *Tamias striatus*, *Citellus tridecemlineatus*, *Glaucomys volans*, and *Tamiasciurus hudsonicus*. They showed that the typical sciurid male tract as seen in all these genera (except *Tamiasciurus*), and as also described by Krölling (1921) in *Sciurus vulgaris*, is characterized by a unique arrangement of the ducts of the bulbo-urethral glands. Tullberg (1899) gave enough information on several other genera to indicate the probability that they also have this same character, and Oudemans (1892) made it fairly clear that *Petaurista petaurista* is essentially like *Sciurus*. So, with the exception of *Tamiasciurus*, other sciurids so far as known have a pair of large bulbo-urethral glands drained by a pair of voluminous ducts which, upon entering the sheath of the corpus cavernosum urethrae in the bulb region, become highly modified to form another accessory organ, the bulbar gland. This whole complex is then drained by a single long glandular duct, the penile duct, which lies ventral to the urethra throughout almost the entire length of the corpus cavernosum urethrae, finally entering the urethra at approximately the base of the glans. The author has examined some other genera, including *Marmota* and *Heliosciurus* and has found them also fundamentally like this.

At the same time we showed that *Tamiasciurus*, the red squirrel or chickaree, possesses an entirely different type of bulbo-urethral gland and duct. It has no bulbar gland and no penile duct. It does have a urethral sinus in the bulb much like that of some Muridae. Later it was shown that the female tract of the chickarees is also unique, the vagina being extremely long and coiled while that of all other Sciuridae studied is short and broad (Mossman, 1940). Other peculiar features of the male tract of the chickarees, such as the long filiform penis and the absence of a baculum, were also pointed out at that time. (Layne (1952) has shown that *Tamiasciurus* does possess a minute baculum averaging only .26 mm. in length in adults. Pocock and the author both failed to note this structure.)

A recent, and as yet unpublished manuscript by Mr. M. R. N. Prasad of Central College, Bangalore, India entitled, "Male genital tract of two genera of Indian squirrels," presents excellent descriptions of the palm squirrel, *Funambulus palmarum palmarum* Linn., and of the giant Malabar squirrel, *Ratufa indica maxima* Schreb. *Ratufa* has the typical sciurid tract, but *F. palmarum* is like *Tamiasciurus* in having minute Cowper's glands and no bulbar gland or penile duct. Obviously this indicates close relationship between this species and the Tamiasciurinae, and poses a number of interesting questions in regard to sciurid phylogeny and geographic distribution, to say nothing of the doubt it throws on the present taxonomy of the whole group.

Although the nature of the reproductive tracts of most of the genera of squirrels is still unknown, enough knowledge is available to make it seem very prob-

able that instead of a wide range of types within the family, there are at least two fundamentally different types. This seems probable as it is definitely known that at least one genus of three of the six tribes that Simpson (1945) includes under the subfamily Sciurinae has the typical male sciurid tract; and that two genera of his second subfamily, Petauristinae, also are typical. One can raise the question then as to the logic in placing the chickarees and Funambulini as tribes of the subfamily Sciurinae when the reproductive tracts of *Tamiasciurus* and *F. p. palmarum* are so different from others of this group. Also, in view of Prasad's work, *F. p. palmarum* and *Ratufa* should not be in the same tribe with one another. Furthermore, it is illogical to place the chickarees and *Funambulus* in these subgroups and at the same time to put *Petaurista* and *Glaucomys* in a separate subfamily, although their genital tracts are almost identical to that of Sciurus. Obviously the flying squirrels (Petauristinae) have been separated on the basis of petagial characters; but these must be highly subject to environmental selection, hence nonconservative. Very similar petagial characters have been developed in certain marsupials (*Acrobates* and *Petaurus*), and in other Eutheria, namely in the Dermoptera, and in the Anomaluroidea among the rodents. Of course one could ask if similar reproductive tract characters may not also have developed in widely unrelated groups. There is no evidence that this is true, but it must be admitted that the data are insufficient. This in itself should be a challenge, to those who ask the question, to make an effort to gather the information.

There may be those who will still fall back on the fundamental question of whether the genital tract characters are more conservative than others in the Sciuridae. If they will allow the ruling out of the genus *Tamiasciurus* and the species *Funambulus p. palmarum* as members of the family, then one can cite the fact that the genital tracts of *Sciurus*, *Tamias*, *Citellus*, *Marmota*, *Ratufa*, and *Glaucomys* are the same in fundamentals, and indeed very similar even in details, while there is great divergence between these various genera in body form, pelage, feet, ears, skeleton, skull, and teeth. If one is not willing to allow the ruling out of the chickaree group, and *F. p. palmarum*, then in the face of the apparent aberrance of these he is bound to withhold judgment until someone can show whether or not there are intergrading forms, so far as male genitals are concerned, between them and the typical sciurids. If there are, then perhaps the genitals are not as conservative as they now seem.

There are a few minor characters of male genital tracts that are variable enough in some groups to be of use in separating species of a single genus. Howell (1938) published a plate showing the bacula of several species each from the genera *Eutamias*, *Citellus*, and *Sciurus*. There are fairly obvious intrageneric differences between these bones within each of the three genera, although occasionally in two species they are practically identical (*Sciurus carolinensis* and *niger*). It is probable that there are other features of the male genitals which would show intrageneric differences: certainly differences in the glans penis correlated with those of the bacula would be expected. However, appreciable intrageneric, species differences in the *internal* genitalia of either the male or female

have never been noted by the author in the sciurids or other groups, but intergeneric differences are the rule, and are often rather extensive; for example between *Tamias*, *Citellus*, and *Sciurus* (Mossman, Lawlah and Bradley, 1932).

To the author's knowledge, no attempt has ever been made to compare the reproductive tract at the level of the higher categories. It seems doubtful that such clearcut indications of relationship would be found as occur in the case of the fetal membranes, where, for example, considerable affinity is shown between the Artiodactyla, Perissodactyla, and Cetacea; and between the Fissipedia and Pinnipedia. Before such a study would be sound, a thorough investigation of the various genera and families of several well-defined orders should be made, in order to evaluate the conservativeness of the various genital tract features.

The female genital tract characters are probably about as equally conservative as those of the male, but those of the female are in general more difficult to observe and define. A good example of this is the os clitoridis or baculum, which in recent years has been demonstrated in females of several species, leading one to expect that, where present in the male, it probably also occurs in the female. This female element may show intrageneric differences like its male homolog, but the fact that it is usually so small and so obviously rudimentary argues against its value as a character for taxonomic purposes. The other characters of the female external genitalia are also relatively indefinite and difficult to observe. Female internal genitalia show a few very definite features which could be of considerable use, but they are almost always too conservative for intrageneric taxonomy, in fact in most cases they are of use only in separating groups higher than genera. For instance, the form of the uterus, oviduct, and ovary is almost identical in the Cervidae and Bovidae. The Mustelidae, Procyonidae, and Ursidae have a peculiar configuration of the oviduct in relation to the ovary and ovarian bursa that is highly characteristic and differs very little between the three families. The Heteromyidae and Geomyidae likewise have a characteristic oviduct pattern which is practically identical in the two groups. By and large then, it may be said that the characters of the female internal genitalia are very conservative, but usually rather obscure and difficult to observe.

Comparative studies of the microscopic anatomy of the ovaries have revealed no case where obvious intrageneric differences exist, except those due to differences in body size of the species. However some intergeneric differences in microscopic structure do occur: for example; ovaries of mature females of *Sylvilagus* and *Lepus* are rather easily distinguished from one another, but those of *Lepus* and *Oryctolagus* would be difficult; *Citellus* and *Sciurus* are separable, but *Sciurus* and *Tamias* are alike, except for size. When one reaches the higher categories such as families and orders, then microscopic features become characteristic for each group. All the mustelids examined have a very similar and typical interstitial cell pattern: this includes *Martes americana*, *Taxidea taxus*, *Mephitis mephitis*, *Spilogale interrupta*, and *Mustela vison*, *cicognani*, *frenata*, and *putorius*. There are even examples of striking similarity in microscopic structure

between related families, at least so far as the few genera of each studied are an indication. Examples of this are Ursidae and Procyonidae, Cervidae and Bovidae, and Erethizontidae and Dasyproctidae.

Let us now turn our attention briefly to the fetal membrane characters of the Sciuridae (Mossman, 1937; Mossman and Weisfeldt, 1939). It is not necessary to enter into a detailed description of the sciurid membranes and placentation, as the main point to be made is that these are even more conservative characters than the male genital system of the group. So it is not surprising that in all the genera studied, *including Tamiasciurus*, the fetal membranes are practically the same, differing only in minor details. These include all the genera mentioned in connection with the male genitals, except *Heliosciurus* and *Petaurista*, and two others in addition, *Cynomys*, *Xerus* (Rau, 1925). In fact the membranes and placenta of *Aplodontia* are distinctly sciuroid, although the male genitals lack the bulbar gland and penile duct.

It appears then that the criteria of the male and female reproductive tracts and the fetal membranes could be applied to advantage in determining the phylogenetic relations of the Sciuridae, and consequently in establishing a more logical taxonomy of this group. The fetal membrane characters are even more conservative criteria than those of the male or female genital tracts.

The application of the genital tract and fetal membrane criteria in the phylogeny and taxonomy of the Sciuridae has been discussed first, since it is the only group in which the author has made reasonably comprehensive studies of both systems. Little has been said thus far of the evaluation of specific criteria, as the studies of the male tract in such a small group do not lend themselves to adequate analysis. The author has however made extensive comparative studies of mammalian fetal membranes and believes, that for them, the basis is broad enough to enable clearly reliable estimates to be made of the relative value of the different characters involved. Since this subject was presented fully in his 1937 monograph, it is not necessary to repeat the details here. Suffice it to point out that all the descriptions of the fetal membranes of specific species which have appeared in the literature since then, and all of the numerous additional observations of the author, bear out the thesis proposed at that time. The facts derived from these studies can be stated very simply.

1. In every group of mammals, high or low in category, in which the members can be clearly related to one another on the basis of total anatomical similarity, their fetal membranes are fundamentally similar, showing far less divergence than do other characters. These groups are perhaps best illustrated by the orders Lagomorpha, Rodentia, Carnivora, and Artiodactyla; by the suborders Microchiroptera, Lemuroidea, and Anthropoidea; by the families Tenrecidae, Soricidae, Talpidae, Cebidae, Cercopithecidae, Pongidae, Dasypodidae, Sciuridae, Heteromyidae, Geomyidae, Muridae, Canidae, Mustelidae, Felidae, Cervidae, and Bovidae; and by numerous genera in these and some other families. All these groups consist of anatomically closely related forms and all have even closer fetal-membrane affinities. They are used as illustrations because enough is known about the fetal membranes of enough members of each group to make

it reasonably certain that the above statement is true. There are other anatomically homogeneous groups such as the Megachiroptera, Cetacea, and Perissodactyla where the limited data available points in the same direction. This is particularly true of the data on the species of numerous genera of the groups already mentioned.

2. In many groups of mammals made up of subgroups widely divergent or of uncertain affinities there are fundamental differences in the fetal membranes. This is true of the Insectivora; the Chiroptera, where there is wide divergence between the membranes of the two suborders (Microchiroptera and Megachiroptera); the Primates, where the membranes of Lemuroidea and Tarsoidea differ widely from one another and from the Anthropoidea; and the Edentata, where the Bradipodidae and Myrmecophagidae are probably much alike, but differ markedly from the Dasypodidae. The Pholidota, often included in the order Edentata, differ fundamentally from all others of this order.

3. The membranes of certain groups commonly separated on anatomical grounds, but known to be somewhat related, are often so similar that the wideness of separation does not seem justified. This is true of the Pongidae and Hominidae, the Lagomorpha and Rodentia, and of the Perissodactyla and Artiodactyla.

4. There are fundamental similarities between certain aberrant groups and other groups to which they have not been supposed to be clearly related. Striking examples of this are the strong resemblances between the membranes of the Bradypodidae and the Anthropoidea; between the Lemuroidea, Pholidota, Cetacea, and Sirenia and those of the Perissodactyla and Artiodactyla; and between the Dasypodidae, Rodentia, Microchiroptera and Soricoidea.

More data than are at present available are certainly necessary to warrant drawing more than very tentative conclusions as to the significance or nonsignificance of these facts, but it is interesting to note that there are many points of anatomical resemblance between lemurs and the hoofed animals, and between the sloths and anthropoids. Certainly taxonomists should not close their minds to the possibility that lemurs are an arboreal line derived from stock ancestral to the hoofed animals, and that their relatively slight resemblance to anthropoids is due to retention of primitive characters in both lines, and to convergence and parallelism effected by adaptation of both to an arboreal habitat. Nor should one close his mind to the possibility that the sloths represent highly specialized edentulous forms derived from the same ancestral stock as the anthropoids.

Now that the general method of application of the reproductive tract and fetal membrane criteria to the taxonomy and phylogeny of mammals has been described and illustrated, one must clear up the important point of the evaluation of the criteria used. The basis for this is the observation described as number 1 above; namely, that in every group of mammals in which the members can be clearly related to one another on the basis of total anatomical similarity their fetal membranes are fundamentally similar, showing far less divergence than do other characters. This makes it possible to compare the variability of differ-

ent features of the membranes within the group as a whole and within its various lesser taxonomic categories, as was done by the author some years ago (Mossman, 1937). Those characters which are consistently constant throughout all the subgroups of a major category certainly are the more conservative ones of that group. If the same characters are also constant, but not necessarily alike, throughout several well established orders, then they are certainly characters conservative enough to be used for establishing phylogenetic relationships between orders. If they are constant within single families, but vary between different families of an order, then they are only conservative enough to establish relationship between families. This general principle can be applied to all categories. Obviously one must choose test groups in which the taxonomy is quite clear and definite, and must compare parallel, major groups in which the minor categories are also reasonably parallel in value. This is obviously arguing in a circle, and thus a dangerous practice if not tempered with good judgment and a reasonable scientific conservatism on the part of the person using it. However it is the best method available, and far superior to making no attempt at evaluation.

One further argument in favor of the fetal membranes as criteria for phylogeny must be stated. This point seems even more important than that of their conservatism. In fact, coupled with their conservatism, it makes them the most ideal of all anatomical criteria for recent forms. This is the fact that the history of the development of the fetal membranes of a species is the history of a complete, complex, and, structurally, highly independent organ system, from its inception during cleavage to its complete functional maturity, old age, and death at the time of birth of the young. We are therefore dealing with the complete life history of an organ system carried out in the relatively constant environment of the uterus, thus almost completely isolated from adaptational demands of the varying external environment. Other criteria commonly used do not offer this overall picture of the individual. The fetal membranes and their development are complicated, but far less so than the total history of all the organ systems ordinarily used as criteria. Their conservatism, and the total developmental picture that they give, render them the most ideal of all organ systems for phylogenetic and taxonomic studies of recent mammals.

SUMMARY

When compared with the organ systems ordinarily employed as criteria for taxonomic and phylogenetic studies of mammals, the characters of the male and the female reproductive systems and of the fetal membranes are the more conservative. This is apparently due to the relatively minor role that adaptation to external environment has played in the evolution of these systems.

Little effort has ever been made to apply male and female genital tract characters to such studies of mammals, but a limited consideration of them by the author indicates that they are less conservative than the fetal membranes. They furnish characters that are of use in the study of the interrelationships of genera and families, and, in some cases, even of species. Whether or not they would be

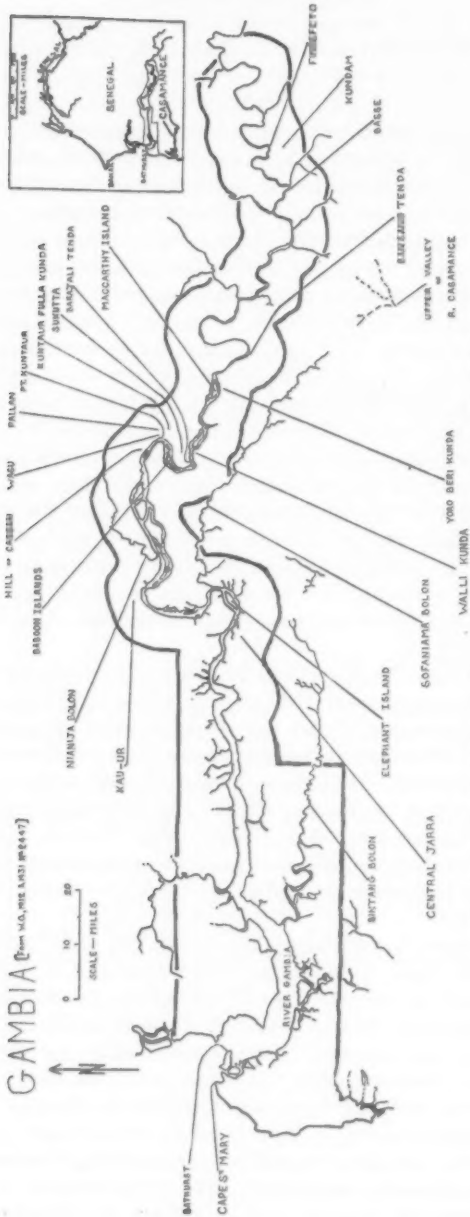

FIG. 1.—Gambia. (INSERT, Gambia in relation to adjacent territories.)

Club, to study, among other things, problems of rice cultivation and hippopotamus control in Gambia. The latter problem was my task.

The expedition received grants from the Royal Geographical Society, the Geographical Magazine, the Oxford University Chest, Alexander Allan Paton Memorial Fund, Balliol, Christ Church, Merton, New, Pembroke and St. John's Colleges, Oxford. (See Oxford University Exploration Club Bulletin, No. 2, 1949.)

The importance of the hippopotamus in African ecology can be visualized when game reports from Uganda are perused. There, at times, as many as 2000 hippos have been counted in 8 miles of the River Nile, and rough estimates have been made from portions of some East African rivers of 50 individuals to 100 yards of river (Uganda, 1937, 1935: 29). As each hippo weighs from one to three tons, such herds must require considerable quantities of grass for food, and must therefore represent considerable competition along the river flats for other grazing species—both domesticated and wild.

The Oxford University Gambia Expedition was stationed during its stay in Gambia at Port Kuntaur, a trading station about 150 miles up the river from Bathurst, from July 20 to September 8, 1948. My own investigation of the hippopotamus in Gambia was thus very brief. A further difficulty was that hippos were scarcer than I had been led to expect; only eight animals were seen with certainty in the seven weeks up-river. Prior to the departure of the expedition from Britain, it had been unofficially reported that there were about 100 animals in the vicinity of Kuntaur, but if this were so, the animals were extraordinarily timid, finding sanctuary in the numerous overgrown bolons (tidal creeks) opening into the River Gambia.

Most of my enquiries were made of people living in villages around Kuntaur with the aid of an African interpreter, who, being with me for long periods, became familiar with my problem. In addition to cross questioning in the villages and in the paddy fields, short trips were made in search of hippos to various localities along the river, or up the bolons. No hippos were seen by me on land during my stay in Gambia. This may have been due to restricted views because of the absence of high ground and the thickness of riverside vegetation, as well as to the scarceness or timidity of the hippos.

In addition to the work done around Kuntaur, five days were spent based at Basse, Upper River Division, and from here trips of enquiry were made to adjacent villages.

While in Gambia, generous help and hospitality were given to the expedition by many administrators. Above all Sir Andrew Wright, then Governor of the Gambia, is to be sincerely thanked for initially suggesting that the expedition should be organised. In Gambia his aide-de-camp, Mr. D. A. Murphy, gave valuable help on many matters. We are indebted to the United Africa Company for letting us live in one of their bungalows at Port Kuntaur during our stay there. While up-river we enjoyed the help and hospitality of Mr. Palmer, Chief Agricultural Officer, and Mr. Hodgson, then Commissioner of Upper River Division, and in particular of Colonel and Mrs. Sealy of Georgetown (on MacCarthy

island). Colonel Sealy solved many of our transport problems while we were stationed at Port Kuntaur, and since the return of the expedition to Britain, he has provided me with some valuable information. To all these people and others unnamed, go the sincere thanks of the expedition for their kind efforts on our behalf. I must also thank administrators in other African territories for answering my queries—Colonel C. R. S. Pitman (Game Warden, Uganda); the Directors of Agriculture, Sierra Leone and Gold Coast; the Inspector General of Forests, French West Africa. Finally I am indebted to Mr. Charles Elton, Mr. Francis Huxley, Mr. Norman Moore, Miss Gillian Godfrey and my wife (Dr. Marianne Fillenz) for criticism of the manuscript. None of the above persons, of course, can be held responsible for the views which I have expressed in this paper.

It seems unlikely that only recently have hippopotamuses and other animals become pests to African farmers along the River Gambia. The fascinating and very realistic picture of eighteenth century Gambia given by Moore (1739) makes it clear that all the faunal and agricultural elements were then present to create economic situations similar to those existing in Gambia today. From this book it seems that all animal life has been considerably depleted in the Gambia since the arrival in numbers of western man, something which is recognised by persons who knew the Colony and Protectorate at the end of the last century, and is only too common elsewhere in Africa.

Rice was certainly grown in the Gambia in Moore's time. On the map at the front of the book there is written across the mouth of the river Gambia "these islands and the parts adjoining. . .produce ye greatest part of ye Rice used at ye factories, the land being low and proper for that." While making a general description of Gambia on page 26, Moore refers to the open ground on either bank of the river where rice is grown. Hippopotamuses or river horses ranged up and down the river Gambia, and were probably much more abundant then than now. But though the elephant is mentioned as a crop pest in Moore's book, apparently the hippo was not then regarded as a nuisance.

DISTRIBUTION AND NUMBER OF HIPPOS

The common hippopotamus (*Hippopotamus amphibius*) is found in most African lakes and rivers south of the Sahara, though it is absent from Madagascar. "In the extreme south of their range they have become local and in most localities are in danger of extinction" (Bartholomew, 1911: 23). The pigmy hippopotamus, *Choeropsis liberiensis*, is found in Liberia, West Africa, extending north to the Mano River and its tributaries at the Liberia-Sierra Leone border. It is said to be rare and of no economic importance. (Mackenzie, 1950.)

The distribution of the hippo over the area south of the Sahara is not uniform. It is very abundant in British East Africa (Uganda, Kenya, Tanganyika) and is probably rarer in West Africa. In the Gold Coast Colony the hippo occurs in only the sparsely populated parts of the northern territory, and causes no significant economic damage there (Miller, 1950). In Gambia the hippopotamus is probably much rarer now than 40 or 50 years ago. It appears to range at least from Elephant Island to the east end of the Protectorate. I saw one animal in the river at Findefeto, Upper River Division, in late August (Fig. 1). It is possible that the number of hippos decreases up river from MacCarthy Island, the increased height and steepness of the river bank making travel to and from the river difficult (however cf. Moore,

1739: 216). At Bansang, where the bank is still quite low, hippos are known to appear quite often. In the dry season, up-river, runways cutting through the river bank are probably used by the hippos when moving onto the land. Bolons would also facilitate the terrestrial wanderings, their banks, a little way from their mouth, being quite low. During the wet season, with the river swollen by flood waters, access to the land becomes simpler for the hippopotamus. For instance, during August, 1948, the river at Basse, Upper River Division, rose at least 15 feet to the top of the bank, flooding parts of the riverside native settlement. In late August or early September, then, hippos would have access to the now well advanced crops beyond, though to battle against the powerful river current must require considerable effort. In spite of this possible tax on the hippo's strength, it is of interest that in August, 1947, there was a request from Basse for the assistance of a native hunter to shoot hippos in that region, where they have been causing damage to rice.

It is generally accepted that hippos are to be found in Gambia as far west as Elephant Island, or in the Badume Swamps in Central Jarra (Lister, 1949). Occasionally they may venture further towards the river mouth; for instance one was shot in the Upper Bintang Creek in 1934, though it is possible that this animal came overland from the river near Elephant Island (Assheton, 1949). During my stay in Gambia none were seen west of Kuntaur, though there were reports of an animal in the river near the Hill of Cassan and in the adjacent Niani Maro Bolon. Whether it is the increased salinity of the river water, or the greater disturbance through the more frequent contact with man, which limits the westward movement of the hippo in Gambia, it is difficult to say. In East Africa hippos, generally speaking, do not seem to be very shy of man. On the other hand, from the Sierra Leone I have a report of hippos frequenting areas below the tidal limit of the Little Scarcies River, and in fact venturing almost to its mouth, where the water is presumably quite salty. Pitman (1945: 100) says the hippo is quite at home in salt as well as fresh water. In the dry season in Gambia, Kau-ur is the last place at which ship crews can be sure of getting fresh water from the river surface, though of course in the wet season fresh water can be got much closer to the river mouth.

It would be of value in the estimation of numbers from uncritical reports to know the extent of the home range of the hippo, and how far up and down the River Gambia an animal can move in 24 hours. I suggest that some of the attacks on the Port Kuntaur-Wasu rice crops during August and September, 1948, were made by animals coming down the river from the south end of the Baboon Islands. When working at Barajali Tenda, hippos were seen in the early morning and evening near Walli Kunda and at the south end of the Baboon Islands, but no animals were seen in the Port Kuntaur region. A few days after seeing the animals at Walli Kunda, hippo tracks were found running through the riverside swamp and paddy near the U. A. C. bungalow (Pl. I). Grass and rice had been eaten, but no further activity in the area was observed. The offending animals had either gone up the river to the Baboon Islands, or up Hona Bolon (one mile south of Port Kuntaur), or west to Niani Maro Bolon near the Hill of Cassan, all places of known hippo activity.

The absence of tributaries of any length running into the River Gambia (bolons are relatively short) greatly restricts the movement of hippos north or southward. There are dry areas of considerable extent between the River Gambia and the River Senegal in the north, or the Casamance in the south. Hippos, if they do not approach the mouth of the River Gambia, can probably travel no more than 10 miles in a northerly direction while yet remaining in or near water of any description, though it may be possible for them to go to the head of Sofanaima Bolon, cross a narrow stretch of land, and enter the upper Casamance River to the south, or to cross into the northern tributaries of the Casamance from the southern branches of Bintang Bolon. (Fig. 1). In any case, movements to and from the Casamance River are more likely than the Senegal. However, though water has been known to act as a very critical limiting factor to hippo herds in East Africa hippos can wander surprisingly large distances over the land, and individuals have been met far from rivers, lakes or water holes. While we were in Gambia, fresh evidence of quite a long overland trek by a hippo was found. In early August a hippo track was followed from the river near Wasu

PLATE I

UPPER LEFT. Hippo track through uncultivated swamp bordering a paddy field, viewed from above. The track is about 2½ feet wide, and the deep imprints of the feet can be seen. Port Kuntaur. UPPER RIGHT. Rice plants eaten by hippo. About six inches of the rice plants remain above the water in the paddy field. Port Kuntaur. MIDDLE LEFT. Regrowth of rice plants after being grazed by hippo. This is the same spot as that shown upper right,

for about one and one-half miles over groundnut crops, through thick grass and scrub, and onto the Senegambia Plateau. I was told by farmers that the animal had walked a further eight miles to the east, as far as the Senegal border. It had then turned around and returned to the river, for the track was clearly double. The journey had been done at night, and there was no sign of the animal having eaten in the one and one-half miles I had followed the track. Local people, incidentally, did say that females sometimes go inland to hidden swamps for calving.

From West and East Africa there are records of considerable movements along waterways by hippos during the wet season, corroborating the suggestion above that damage at widely separated parts of Gambia may be done by the same small herd. In the *Nigerian Field* (1940: 14) it is said that "Hippo probably move considerably in the wet season in country liable to flooding. Hunters reported the occurrence of Hippo in the upper reaches of the Ogun southeast of Shaki during the rains. There are most certainly none here during the dry season and it is surmised that they must come from one of the Niger tributaries."

Hippos are not usually to be found at Mushongero, on Lake Mutanda in Uganda, but over a number of years up to 1935 a party of three hippos periodically visited the locality, staying a few days before departing. About five such visits were made each year (Uganda, 1935: 29). In 1935 Lake George and certain other localities in Uganda were greatly overcrowded with hippos. It was considered a consequence of this that a large number, representing the surplus, moved up the rivers Mpanga and Wimi to crater lakes, because of the overcrowding elsewhere (*loc. cit.*). In Tanganyika hippo tracks have been followed overland 20 miles, from one river to another, again indicating the possible range of the hippo (Tanganyika, 1933: 8). (For other information on overland travels of hippos see Stevenson Hamilton, 1947: 57, 62-63; Kenya, 1910-11, 1913-14).

Unfortunately, the number of hippos in Gambia is not known with any certainty. Africans were not to be relied upon in their estimations, this being made quite clear by the rather poetic report of the Alkali of Barajali, who considered that "the numbers of fish was not greater than the hippos." (Estimates by Europeans in Gambia range from 1000 to 100 along the river, the latter figure being regarded as the more likely.)

Mention has already been made of the much larger number of hippos to be found in East Africa. The number of hippos shot and the weight of hippo teeth handled in certain years in some East African territories gives a further graphic picture of the abundance of these animals in East Africa (Table 1, 2). It is contended by some that, as with the slaughter of elephants in East Africa, only the surplus of hippos is being killed. But this is only guesswork, an insufficient basis for game management, and points to the necessity of a detailed study of the biology of the hippopotamus.

I have pointed out in this section that though hippos have been known to travel long distances overland, it is unlikely that there is any exchange of animals between Casamance, or Senegal, and Gambia. The hippos in Gambia are an isolated population, although in addition to possibilities already discussed, it must not be ruled out that hippos from Gambia, Senegal and Nigeria meet, rarely, in the Futa Jalon, the high country in French Guinea in which these rivers rise.

Though the number of hippos in Gambia is small, the surprising mobility of the animal,

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but ten days have elapsed and most of the rice plants have completely regrown, reaching above the waists of the two women. Behind the women can be seen an anti-hippo fence. Port Kuntaur. MIDDLE RIGHT. Hippo damage to rice crop. The boys are playing in a bare area which prior to the hippo invasion, had been uniformly covered with rice plants. Barajali Tenda. LOWER LEFT. Grazing of natural grasses by hippo, said to have visited the area two to four days before the photograph was taken. The man in the foreground stands at one edge of the grazed area. The man in the background stands, for comparison, in ungrazed grass reaching almost to his waist. Nearby there were tracks and faeces. Port Kuntaur. LOWER RIGHT. Fence designed to keep hippos from rice crop. A thick growth of young rice is seen in the foreground. Port Kuntaur.

as judged from reports in East African game department journals, would allow a small herd to do widespread damage over a considerable length of the Gambia River. If a small herd, or a number of small herds are operating in Gambia, local shooting could easily wipe out the hippopotamus in the Protectorate.

TABLE 1.—*The number of teeth and their weight, either found or obtained from hippos shot in Tanganyika during the years indicated*

YEAR	SHOT			FOUND			TOTAL NO. HIPPOS REPRESENTED
	No. teeth	Wt. (lbs)	Hippo equivalent*	No. teeth	Wt. (lbs)	Hippo equivalent*	
1937	3,737	1,982	110	878	541	30	140
1936	7,910	4,324	240	491	366	20	260
1935	6,208	3,531	196	1,570	965	54	250
1934	15,024	7,563	420	874	714	40	460
1933	10,613	5,279	293	2,141	1,394	77	370
1932	3,555	1,938	108	2,246	1,568	87	195

* The translation of weight of teeth into number of hippos, i.e. "hippo equivalent", has been made on the basis of a statement in Uganda (1947: 20) that "the average weight of marketable teeth per hippo is about 18 lbs. One ton of hippo teeth represents about 125 hippos."

Data taken from table in the Annual Reports of the Tanganyika Game Department.

TABLE 2.—*The weight of hippo teeth annually exported from Uganda (See Table 1 for a note on "hippo equivalent")*

YEAR	WT. OF HIPPO TEETH EXPORTED	HIPPO EQUIVALENT
1939	1¾ tons	217
1938	2¾ tons	341
1937	3 tons	375
1936	3½ tons	437
1935	2,278 lbs.	126
1934	1,393 lbs.	77
1933	1 ton	125
1930	2,250 lbs.	125

Data taken from the Annual Reports of the Game Department, Uganda (Export Permits).

HIPPOPOTAMUS ACTIVITY AND DAMAGE TO CROPS

In Gambia, hippos move around on land in search of food during the night, this activity commencing in the late afternoon and continuing until about 10 A.M. on the following morning. The remainder of the 24 hours seems to be largely spent lying up in some secluded spot —under overhanging palms on the edge of the river, up bolons, or even in wallows in the middle of swamps. However, feeding has not always been confined to the hours of darkness. Africans told me that it was possible, before there were so many people working in the fields, to see hippos in the swamp during the day, and that in those days the animals were not frightened by passing steamers.

One African farmer at Port Kuntaur considered that the tide, which is appreciable thereabouts, affects locally the terrestrial wanderings of the hippo. When the tide is high the animals can easily scramble up the river bank, but when low they find this difficult.

Any possible tidal effect such as this would be more apparent in the dry season when the river is low, than in the wet. During the dry season it could conceivably impose a rhythm of activity on hippos. In the wet season, with the river swollen by flood waters and the bank consequently very much reduced, there is probably no landing difficulty for the hippo. In any case there are inevitable breaks in the river bank from place to place, and if confronted with a high bank, the animal could get on land by way of a bolon.

Damage in Gambia.—Rice grown in Gambia is almost entirely of the swamp variety, requiring its roots to be flooded during growth. The crops are thus confined to the narrow alluvial stretch on either side of the River Gambia, up to a mile wide, with perhaps smaller areas further inland along bolons.

The effect of the hippo on rice production in Gambia seems to be both direct and indirect. The hippopotamus is said to attack rice crops only when they are coming into head, that is in October, and to destroy by this trampling and eating enough rice to feed ten men for a week. The harvest in Gambia continues from October until December or January. Unfortunately, the Oxford University Gambia Expedition returned to Britain in mid-September, when some rice was still being transplanted from village nurseries, and other crops, though four or five feet high, were not yet in head. However during August I witnessed several minor attacks on rice crops at Port Kuntaur, Wasu, Madina (one-half mile north of Wasu), Barajali Tenda, and possibly crops of the village of Kundam, one and one-half miles inland from Findefeto, Upper River Division. The absence of more extensive damage to crops may have been because the crops were not yet to the hippos' liking, or it may have been the utmost that could be expected of the small number of hippos living in the river at that time. In any case, it seems that damage to rice crops is most felt in the period October to December. Rice eaten before this, not yet in head, has a chance of regrowing in time to be productive before the onset of the dry season (Pl. I). Of course it must be remembered that the damage to rice crops by the hippo is not confined merely to eating; there is also the trampling and breaking of plants as the bulky animal moves through the crop (Pl. I).

In the first week of August a hippo was active on the river bank north of the U. A. C. bungalow, Port Kuntaur. Though rice is nearby paddy fields was two or three feet high and quite accessible, the animal confined its attention to grass, grazing to within six inches of the ground, or less, but not apparently pulling it up (Pl. I). (The hippo is said to pull up rice in grazing.) Two weeks later in the same region rice had been grazed, the shoots, probably three feet above the one to two feet deep water covering the paddy, having been bitten off one to four inches above the surface of the water (Pl. I). A number of tracks two and one-half to three feet wide, in themselves representing considerable loss of rice, were clearly visible in the crop and in the adjacent uncultivated swamp (Pl. I). Ten days later this rice had regenerated almost completely, the tops of the plants being four feet above the water and only with difficulty distinguishable from the originally ungrazed plants (Pl. I).

A word is necessary about the identification of rice plants which have been grazed by hippos. ("Chopped" in the vernacular.) It is the practise of Africans in Gambia to cut off about the top six inches of the rice plants grown in the nurseries before they are transplanted. When first seen such shortened plants might be mistaken for hippo-damaged material. However hippos, in my experience, graze the rice much closer to the water, the cut edges are less regular than those of the transplants whose tips are about one foot above the water, and in any case there are usually to be seen the tell-tale foot prints of the hippo in the damaged crop (Pl. I).

The riverside swamps in Gambia, on some of which rice is grown, are extensive, being at least three hundred yards deep and stretching along the river bank as much as half a mile before being cut off from similar flats by a narrow belt of trees, running perhaps along a bolon. Such regions, sometimes opening onto the river without the interruption of a riverside growth of trees, are covered with sedges, phragmites, and various other grasses. There may be a few clumps of raphia or fanjano palms along the river bank. By August or September the sedges and grasses have grown to ten or twelve feet, and present an obstacle

to walking, particularly as under-foot the ground is broken and waterlogged. In horizontal succession from the river, the ground rises slightly and gradually, and a quarter to half a mile inland from the bank, swamp may be replaced by a mixed stand of palms, baobabs, silk cotton trees and an occasional mahogany, or more rarely by a fairly pure stand of *Acacia* scrub.

It is surprising how little of these riverside swamps is cultivated. At several villages, close to which such strips occurred (e.g. Sukutta, Barajali, Barajali Tenda), I was told that they were good rice growing areas. Two factors which contribute to their being incompletely cultivated are fear of hippo damage to crops so near to, and easily accessible from, the river, and labour and distance. For a very long time rice growing has been the occupation of women in Gambia. Moore says: "The Evenings and Mornings were very foggy, and the Women busy in cutting their Rice; which, I must remark, is their own property; for after they have set by a sufficient quantity for family use, they sell the Remainder, and take the money themselves, the Husbands not interfering. . . ." (Moore, 1739. p. 98). Even now it is the means by which women get a little money of their own, besides supplying the village with some rice. But rice growing is hard and unpleasant work, and the men spend most of their time attending groundnuts and koos. Until they work more in the paddies, rice production will be inadequate.

Damage elsewhere in Africa.—There are plenty of records in the journals of the East African Game or Agricultural departments drawing attention to the genuine damage done by hippos to crops. Nearly every number of a Ugandan Game Department Journal, for instance, will mention hippo activity in cultivated areas.

It is recognized in Uganda that because the hippo has to come ashore to feed, if access to suitable grazing is denied by crops which, in any case may have taken the place of natural food, then there is certain to be trouble (Uganda, 1934: 19). It has been suggested that a system of cultivation in which crop lands are frequently abandoned induces a type of vegetation particularly attractive to the hippopotamus. This may explain the animal's attachment to the abode of man (*loc. cit.*: 1929: 23). In Uganda in 1934 the large numbers of hippos along parts of the Victoria-Nyanza coast were regarded as constituting a direct threat to efforts being made to reclaim some of the fertile littoral for resettlement. Real setbacks were recognized along the Entebbe shore, and an inclination was recognized, among those (? Africans) participating in the scheme, to abandon the project (*loc. cit.*, 1934: 19).

Whereas in Gambia complaints are lodged because of attacks on rice alone, in Uganda, damage to sweet potatoes, matama and wimbi crops is also recorded (*loc. cit.*, 1935: 29). Reports of the Warden of the Kruger National Park give records of vexing damage to farm crops (Kruger, 1941: 10; 1934: 12). However in spite of certain well attested cases of hippo damage to crops, "the hippopotamus owing to the attention attracted by its bulk, continues to enjoy an undeserved reputation for ferocity coupled with that of a perpetrator of excessive damage." (Uganda, 1929: 33). It is also said (*loc. cit.*), in reply to complaints of serious damage to crops along the shores of the Victoria-Nyanza, that "judicious pitting would speedily abate the nuisance."

PREVENTIVE MEASURES

Shooting.—The skull of the hippopotamus is very thick, also the hide, so that high powered rifles are necessary in shooting the animals. In Gambia a .303 rifle has been available to an authorized African hunter. Some of the men in most Gambian villages possess native shotguns. These are ancient instruments for which shot and powder are issued annually for the destruction of baboons and other crop pests. Native shotguns, however, would be hopelessly inefficient against hippos, possibly only enraging them.

Fences.—There is some conflict of opinion in Gambia about the ability of a hippo to overcome minor horizontal obstructions in its path. Some say that a light-weight tree branch placed horizontally a foot or two above the ground is sufficient to deter a hippo. When the colossal bulk of the creature is considered this may seem extraordinary, but sim-

ilar structures, used in the Kruger National Park to reduce damage along the Crocodile (Limpopo) River, seem to have been effective. The Warden of the Park reports that a very low fence is sufficient to deter a hippo; the animals do not seem to step over very low obstacles nor to push through a wire fence. (Kruger, 1935: 15; 1941: 10; 1940: 14; Stevenson Hamilton, 1947: 57–58.) From Dr. Haddow of Uganda, I have learned in conversation that in Uganda low, light-weight, horizontal bars are erected in many areas and seem to be effective in excluding hippos from crops.

There is a widespread fatalism amongst Africans in Gambia concerning the effectiveness of fencing. This stems from the attitude that "Marlo (the hippo) can push down anything!". None-the-less several sorts of barricade are constructed.

Most commonly a flimsy fence is made by pushing boughs, one to three inches in diameter, into the soft mud on the edge of the paddy fields at about four foot intervals. These stakes stand about three or four feet above the water and are joined by similar horizontal boughs lashed to the stakes with native twine (Pl. I). The fences may be built around only two sides of a paddy field, so that even if strong enough to resist an oncoming hippo, the animal could easily enter the crop from the unfenced side. It is said by Africans that hippos are powerless to push over fences that are built right on the river edge, and with which they are therefore confronted while still emerging from the river. But once on land, the African will continue, their power is considerable, so that, though a farmer may diligently fence all sides of his paddy field, a hippo may come on land in an adjacent unfenced area, walk to the fenced paddy, and push down the barricade quite easily. To have full protection the whole river needs to be fenced, say the farmers, and because this is impossible, practically nothing is done by them.

A much stouter barricade is sometimes placed across hippo landings on the river bank. It consists of two forked tree trunks, six to 12 inches in diameter, sunk in the ground on either side of the landing, with a third trunk, up to six feet long, laid in the forks and stretching across the gap. If it is true that the hippos are unable to land except where the bank has been broken down by man or erosion, then these blocks would be effective.

At the Yora Beri Kunda experimental rice plot, on the bank of the Gambia River, wooden stakes, I was told, had been driven into the river bottom close to the bank along the river front of the rice plot. The tops of the stakes were approximately flush with the top of the bank. The spaces between the stakes comprising this underwater palisade, were presumably less than the width of the hippo's feet, so that the marauding animals would be unable to get a grip on the bank, preventing them from landing at this point.

There is an adequate supply of timber, suitable for fence construction, near every Gambian rice-growing village, but two things have to be overcome. Firstly, the apathy and scepticism of all farmers, who think that, even if "marlo" does not push over the fence, the posts will float away when the river floods the banks during the wet season. Secondly, the men must be persuaded to take a greater interest in rice growing. The hard work involved in fence construction around paddy fields, situated some miles from the village, cannot be effectively done by women, who are already burdened, not only with a great deal of rice cultivation, but with duties in the village life. Significantly enough I have been told by Africans that fence posts used are "no heavier than a man could carry."

In East Africa there is, amongst some African farmers, an attitude of helplessness requiring other people to solve agricultural problems. This is emphasized in Uganda (1938: 24) where it is pointed out that the African farmers often exaggerate the damage done to their crops, that though there is an abundant timber supply they make little attempt to build protective fences, and that all too readily they seek help from and make complaints to the Government (see also Pitman, 1945: 98). In this way, as in others, the situation in East Africa resembles that in Gambia.

Marginal swamp strips.—It seemed both from observation and from conversation that in some cases a strip of untouched swamp, up to forty yards wide, was sometimes left between the river and the rice fields in Gambia. This, some people said, was to protect the crops from hippos, putting a food buffer of natural grasses between them and the rice.

However the existence of such uncultivated strips along the river's edge may be because they are liable to excessive flooding during the wet season and therefore unsuitable for rice cultivation. It does seem unlikely that such a strip of virgin swamp would keep hippos from rice crops, when their ability to roam on land is remembered. The strip of land suitable for the cultivation of rice on either side of the river is so narrow that, by providing a buffer of adequate width, the best paddy areas would be eliminated. Further, such marginal strips would often carry thick riverside forest, which would directly oppose some methods of tsetse fly control, just as important to the population as hippo control.

Possible natural barrier.—On the banks of the middle Gambia grow, besides several other types, what local people call fanjano palm, *Pandanus candelabrum*. Inpenetrable thickets of these, reaching a height of about 30 feet, are to be seen stretching sometimes several hundred yards along the bank of the river. According to some Africans, by the time the more rapidly growing central part has produced a seed case, it is itself dry like tinder. The seed case ruptures and the process of splitting starts a fire. The centre of the palm is burnt out, but the younger, peripheral parts, being green, are saved. Later these in their turn dry out and catch fire in the same way, by which time, however, the original burnt out centre has largely regrown. Opposite Barajali Tenda, in August, a palm was seen whose centre was burnt out, apparently in this manner, but whose edges were still green.

The fanjano has thorns on its leaves and stem, which some people think are sufficient to deter hippos from pushing through thickets. When the thickness of the hippo's skin is considered (one-half to one inch dorso-lumbar, dorso-thoracic) this seems unlikely.

The fanjano, when well developed, spreads, at a height of about two feet, horizontally over the water as much as fifteen feet, and these low overhanging branches send down a network of roots to the river bottom. Though it has been reckoned unlikely that fanjano *thorns* would be sufficiently unpleasant to stop a hippo from walking through a thicket, it does seem likely that the *tangle* of branches and leaves characteristic of fanjano growth, would make passage through the thicket impossible for any but the smallest of mammals. However, in spite of this, it was said in some villages that "marlo" rests beneath these palms.

The palm is said to grow from cuttings, and bearing in mind their prolific growth along certain parts of the Gambia (e.g. near the south end of the Baboon islands) while yet being confined to the river bank, it is possible that these could form an effective barrier against hippo invasion in rice growing areas. Immediate disadvantages are the supposed self generated, periodic conflagrations, and the shelter provided under such riverside thickets for tsetse flies. But I feel that, if there is great need for hippo control in Gambia, while still maintaining their numbers, a search should be made for such natural barriers.

In Kenya, temporary relief from elephant raids has been obtained by tying empty kerosine tins, or expoding maroons, along well used elephant tracks. The noise of clanging tins, or of explosions, was a successful deterrent for a while, and in the case quoted, was succeeded by shooting measures (Kenya, 1937: 16).

Hippo as food.—Certainly the hippo does appreciable damage to rice crops, but there is probably an additional motive behind the killing of hippos by Africans, or the demands that they should be killed. Gambian natives have a diet which is very meat-deficient, so that the addition of a ton or two of hippo flesh, which is very good eating, to the village supplies, would meet with approval. It is clear that other animals (baboons, other monkeys, bush pig, weaver birds), either less palatable or less profitable as food, are doing as much or more damage to rice and other crops as is the hippo. Natives realize the menace of these animals, but it is my belief that they emphasize the hippo more because of its food value. The esteem with which the hippo is held by Africans as food was dramatically shown by the almost complete disappearance of a hippo shot near Port Kuntaur in early September, 1948. The only portion of the animal left after about two hours activity by thirty or forty Africans was the head. Everything else, including all parts of the viscera, had been taken for food or other purposes.

In an inverse way the food motive affects pest control in East Africa. In Tanganyika,

during 1935, the average native cultivator knew that ". . . if he complains to his District Officer, he will, if possible, be given immediate assistance against elephants and large mammals, but baboons, pig, etc., are his own little pigeon and he must deal with them himself. To shoot them with his old loader (if he has one) is to his way of thinking a mere waste of powder and iron bullets, as he does not eat the meat, at any rate not of the baboons. Bush buck and reed buck, which also raid from time to time, are a different matter. They can be eaten, therefore very few complaints are received about the last two animals." (Tanganyika, 1935). In the case of hippos, native loaders would be inadequate, even under the added stimulus of more meat. For this reason, and unlike the situation just reported for Tanganyika, I consider that complaints about hippos are intensified in the hope that animals will be shot with a Government rifle, and the carcass, too heavy to remove, will be left for the Africans. Stevenson-Hamilton (1947: 62) states that motives for killing also include the value of hide and ivory.

NATURAL CONTROL OF HIPPOPOTAMUS POPULATIONS

From a study of the reports of several East African game departments and from scanty knowledge of the conditions in Gambia, it is possible to gain some picture of what biotic and physical factors are operating to keep down hippo numbers. Actually the effect of the various factors seems mild; for instance, there are only two records of the outbreak of disease in East African hippo herds, and none, so far as I know, in Gambia. If fewer hippopotamuses were killed each year by man, then it is possible that from time to time outbreaks of disease would decimate the resulting much larger herds. It so happens that, as is supposed to be the case with the elephant, only the surplus of hippos is apparently being killed in East Africa, and a large breeding population appears to remain. A frequent report in East African journals is "Hippo continue to increase steadily. . . ." or "In spite of annual toll, no noticeable diminution in numbers." (Uganda, 1939: 10; 1936: 26; 1937: 21.) See also Tables 1 and 2.

Biotic factors.—Predators. Crocodiles are plentiful in the River Gambia, but are unlikely to be a serious threat to hippo numbers. Pitman (1945: 119) suggests that crocodiles are serious enemies only to unguarded calves, but there is a report of a midstream battle between a hippo and a crocodile, with, in this case, the hippo victorious (Uganda, 1934: 43). On the other hand it seems that on the banks of Lake Rukwa and in the Sangwe River, in Tanganyika, hippopotamuses and crocodiles tolerate each other's presence (Tanganyika, 1932: 3; Uganda, 1931: 11). In any case crocodiles are said to be unable to bite through the tough hide of freshly killed hippos, but begin on the softer parts. (Tanganyika, 1933: 9)

In Uganda (1934: 43) and Stevenson-Hamilton (1947: 138) there is a report of a young hippo being killed by a couple of lions. Lions and leopards are indigenous to Gambia, but though a large lion was killed near Port Kuntaur in August, 1948, and at about the same time one or two others were reported in the MacCarthy Island Division, these were rather outstanding faunal events for the year. Lions and leopards are regarded as scarce in Gambia today. It is possible that the success or failure of the wet season in Senegal or Casamance influences the number of terrestrial predators, besides other animals, in Gambia. As mentioned later, the river is a fairly dependable source of water, so that during the long dry seasons and poor wet seasons—seasons such as Senegal is said to have experienced in 1948—lions and leopards could be expected to roam into Gambia. "During the dry season, lions are very plentiful in the vicinity of the Greek River in the Eastern Province." (Uganda, 1936: 21). However it seems unlikely that, unless several lions, leopards, or crocodiles simultaneously attacked an adult hippo, such an impregnable beast would succumb to these predators, whose toll, if any, must be largely confined to calves.

Elephants have at least some fright value. There is a report in Uganda (1929: 7) of the panic-stricken rush of about 50 hippos caused by "two magnificent tuskers" stepping out of the adjacent bush amongst them.

Disease. Anthrax is thought to infect elephants and perhaps regulate their numbers. A similar micro-organism might well be looked for in the hippopotamus. In the year 1932–

33 there was reported in Uganda the mysterious, sudden death of hippos in Lake Albert. The outbreak was short in duration and was rather naively suggested as due, possibly, to oil seepage (Uganda, 1933: 35). In 1936–37 there was an outbreak of disease amongst the large number of hippos in the Kazinga Channel and in Lake George in Uganda. Again the outbreak was of short duration, but was swift in action, and it was suggested as due to bacteria of the food poisoning group (Uganda, 1937: 21, 32).

It is, of course, well known that hippos serve as reservoirs for certain trypanosomes, but it does not follow that the animals succumb to trypanosome disease (Hale Carpenter, 1913, 1920; Duke, 1912).

Fighting. The large lower canine teeth of the hippo make effective weapons for attack on other animals, whether of the same or of a different species. It has been suggested that the mortality of the juvenile hippos of Lake Edward may be due to bulls attacking youngsters. Dead specimens found in the lake in 1929 were usually pierced in the heart region, and there were no crocodiles in the lake. The ferocity of males and females in the mating season is well recognized, and it is suggested in reports that damaged animals leave the water because of fish nibbling at wounds, roving then at large (Uganda, 1929: 33; Tanganyika, 1933: 8).

Only recently has the importance of intraspecific fighting in the regulation of the numbers of animals been recognized (Errington, 1946; Chitty, 1952). It is quite possible that, in those regions of East Africa where hippopotamus numbers are considerable, fighting between members of the herd could assume important proportions in population control. In fact Stevenson Hamilton (1947: 61), writing from his experiences in the Kruger National Park, says "The hides of practically all old bulls are seamed with scars of war." If the situation is anything like that supposed to be the case with some other, smaller, mammalian species, there would be considerable juvenile mortality under the conditions of crowding.

Physical factors.—Depth and flow of water. In Gambia, physical factors probably play little part in hippo control, though the long, dry season would be a critical period. The river is deep and relatively quiet flowing in the Protectorate; there are rapids only in its upper reaches. Water in it is never reduced to a dangerously low level, though during the dry season salt tidal water can be detected further upstream than during the wet season. However information from the Sierra Leone suggests that hippos can tolerate estuarine water. Temperature would only be an important limiting factor if water supplies were inadequate.

In the Kruger National Park, the absence of wide, deep, and slow-flowing rivers with long reaches, which the hippo favours, appears to be acting as a limiting factor in the growth of the hippo population. There are a few deep pools of the right sort, but they are generally separated by miles of broken water. The hippos have been undisturbed for about 35 years, but their number has not increased. Any surplus probably moves into Portuguese East Africa (Kruger, 1935: 7). With the silting up of the rivers due to abnormal flooding, hippopotamus herds break up, the animals ranging more widely. This results in more widespread damage to farm lands. After a spell of several years without floods, giving the pools that had previously been inhabited a chance to rejuvenate, the herds probably resettle in them. (Kruger, 1941: 10; 1940: 14; Stevenson Hamilton, 1947: 62).

That wide expanses of water are the most favourable habitats for hippos is further supported by a report from Uganda that most of the smaller lakes and rivers have hippopotamuses in them "provided there is a sufficiency of open water." (Uganda, 1926: 45). According to other reports the water must not be too deep (Uganda, 1934: 33). There must be a sufficiency of shallow water, eight to ten feet deep being the supposed optimum. On the other hand, in Gambia, hippos were seen quite often at the south end of the Baboon Islands, where the water is much deeper than this, being up to six fathoms in the wet season.

The fatal effect on hippos of the drying up of pools has recently been dramatically illustrated in Picture Post (1950). Also during 1946, pools in Tanganyika, in which hippos normally spent their days during the dry season, dried up, and many animals died.

With the hippo population at its present low level in Gambia, food during the critical

dry season, I was assured, was abundant enough along the banks of the river. In Kruger (1934: 12) is mentioned damage to crops during the dry season when food is scarce along the river bank.

CONCLUSIONS

Vogt (1949) and Roberts (1951) have issued grave warnings about the over-population of the world, and remind us that the earth has a limited carrying capacity. Over-population and unscrupulous business operations have meant the wastage of great areas of forest and grassland, the recovery of which may take longer, perhaps, than the world's present day timber and food shortage will allow.

Africa has suffered in the same way, though not so severely, as North and South America, the countries about which Vogt largely writes. European as well as African population increase has meant more and more strain on African resources. Recently the world has witnessed the extensive clearing of land in East Africa in connection with the groundnut scheme. The cutting of timber in West African forests, and the shooting of game both for sport and for the protection of property have been and are activities of man in Africa which are threatening the continent's fertility. There has been a more concentrated attack on the tsetse fly in Africa in the last ten years, a great diversity of control methods being employed, with considerable impact on elements of the fauna and flora. The reduction of sleeping sickness mortality may well prove a mixed blessing to Africans of the future, as has been malarial control in other parts of the world; that is, unless some sort of birth control can be introduced, which seems unlikely enough. Otherwise people may survive only to die later of starvation.

Vogt has said that Tanganyika Territory enjoys two advantages, a low population and sleeping sickness. He points out that over large parts of Africa the water table is falling, and that rain forest is being replaced by savanna, savanna by thornbush, steppe, and desert. There has been a regression of the forests of the Gold Coast since 1908, but the rich savanna, he says, is the most vulnerable. It is generally overpopulated, so that, with intensive but unscientific farming, the ground, by the beginning of the long dry season, is in no state to be subject to the strong dry winds. Cover, in tropical and sub-tropical Africa, is invaluable in reducing gullying and sheet erosion during the wet season. Vogt further points out that vegetation exploitation has meant the destruction of native animals, and, that aquatic and semi-aquatic mammals and birds have been driven south with the advance of the Sahara.

Before the advent of western man, herds of game in Africa had their numbers regulated by water holes and predators. However with the high prices paid by furriers for leopard skins, with the improvement of weapons available to Africans, and with the amusement which western man has found in hunting lions, there are probably fewer predators. If water holes dry up some animals die and others are left in a weakened condition.

In Gambia there does not yet appear to be a severe erosion problem. The country lies in the vulnerable savanna belt, and great care will have to be exercised over the use of her resources. For instance, if Ngama is reduced with the

development of antricide, and if, as a consequence, cattle herds are increased, there will be a great danger that symptoms of overgrazing will develop. Though the population of Gambia is large, it is still possible for fallowing to be practiced, enabling land to recover after rice and groundnut cultivation.

However, self-sufficiency in rice may be urged for Gambia. To accomplish this, not only will hippos have to be shot, but also baboons, bush pig, and weaver birds, or else fences and other crop protection devised; or finally the country's population may have to be decreased.

If extensive fencing of rice plots to reduce hippo invasions is instituted, then trees of the savanna belt may have to be cut down to provide materials. The growth of grass which would follow such deforestation might be sufficient to check erosion, but there will be the temptation to put more cattle into such cleared areas, thus reducing even the grass cover. If such measures are undertaken, great care will have to be exercised from the start. By proper supervision it may be possible to combine forest management with hippo control.

It is essential that the hippo should survive in Gambia. The destruction of a species is final, and if extinction in West Africa is encouraged, East Africa may find it necessary to lose her much larger herds. Sufficient justification for hippo survival is in the quaintness of the creature, and the possibility of studying its biology in detail. But further, to let one animal be crossed off the West African list of species is merely to hasten the transformation of the country into a desert. It has been suggested to me that hippos, by their movement to and fro, may keep streams free from excessive weed growth. They may, then, keep bolons flowing into the river Gambia, and thus prevent or reduce the extent of flooding of the land and the dragging of soil to the sea in flood and tidal water. With a fuller understanding of hippo ecology, more facts would certainly come to light to justify, in economic terms, the conservation that is called for.

SUMMARY

During the summer of 1948, an expedition organized by the Oxford University Exploration Club went to Gambia, on the west coast of Africa. Among other things, the role of the hippopotamus in the destruction of rice crops in the Protectorate was investigated.

In spite of reports to the contrary, there appeared to be very few hippopotamuses in Gambia at that time. Few direct observations of them were made, but damage done by them was seen, measures taken by local farmers to reduce damage were investigated, and Africans were questioned upon the problems of their rice farming.

Though the hippopotamus does damage rice crops in Gambia, it is suggested that the extent of the destruction is exaggerated in order that hippos will be shot and their greatly-prized meat will become available locally. Because they are less palatable, other animals, such as baboons, other monkeys, and weaver birds are overlooked, although, even separately, they may do as much damage as hippos.

An analysis of the probable biotic and physical factors controlling the number of hippopotamuses in a region is made.

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STOMACH CONTENTS OF CHIPMUNKS AND MANTLED SQUIRRELS IN NORTHEASTERN CALIFORNIA

By Lloyd Tevis, Jr.

A study of feeding habits is important to an understanding of the rodent factor in forest ecology. But a mere list of foods does not indicate the complexity of interrelations between animals and food supplies, which differ markedly in kind and amount from place to place and vary enormously between seasons and from one year to another. Interpretation of the data is necessary.

This paper attempts an interpretation of stomach analyses of 509 chipmunks of four species (*Eutamias amoenus, speciosus, townsendi*, and *quadrimaculatus*) and 273 mantled squirrels (*Citellus lateralis*), which are important kinds of diurnal rodents of the commercial timber belt of northeastern California. The area studied lies within a thirty mile radius of Quincy, Plumas County, California, where the granitic Sierra Nevada meets the Great Volcanic Plateau to the north and the arid Great Basin to the east. The merging of these vast geographic regions creates a complicated and congested biota; for many species come together which are widely separated elsewhere. Some habitats are occupied by all four kinds of chipmunks as well as the mantled squirrel.

The forest is composed of ponderosa, Jeffrey, and sugar pines, Douglas fir, white fir, and incense cedar. It has been subjected to every degree of logging, and is broken by brushfields that are the heritage of disastrous fires. The chief shrubs of Volcanic and Sierran brushfields are manzanita (*Arctostaphylos patula*) and whitethorn (*Ceanothus cordulatus*).

The technique of stomach analysis was described in an earlier paper (Tevis, 1952). The main point to be noted here is that the food was classified into types. An attempt was made to learn which foods maintained high numbers of rodents, to determine seasonal trends in feeding habits, and to compare the diets of different species. The work was done as part of an investigation of the influence of rodents on reforestation conducted by the Department of Zoology, University of California at Davis in cooperation with the California Forest and Range Experiment Station of the United States Forest Service. I am grateful to Dr. Tracy I. Storer for advice and assistance.

Specimens were collected in 1951 from mid-March, when hibernators appeared, until the third week of the following September. This paper, then, is an account of feeding habits during one year. No two years are alike, and a summary of the main features of 1951 follows.

In spring—when occasional rain hastened the melting of patches of snow—surface fungi (*Gyromitra, Peziza*, and *Morchella*) were locally abundant, forbs and grasses greened the forest floor; one of the earliest of the herbs, a figwort, set quantities of seeds; manzanita yielded the heaviest flower crop in years; winged termites emerged from rotten logs on sultry afternoons; and ants and spiders were numerous.

In summer—a season of warmth and of dry ground—the fruits of gooseberry and bitter cherry ripened more abundantly than they had in many seasons;

whitethorn produced large amounts of seed; a gall-forming aphid destroyed a potentially enormous crop of manzanita fruit; new needles of white fir were infested with an aphid; one of the largest outbreaks in years of the California tortoise-shell butterfly defoliated whitethorn over hundreds of acres; and hypogeous fungi increased as surface kinds disappeared.

TABLE 1.—*Percentage volume and (in parentheses) percentage frequency of types of food in stomachs of chipmunks and mantled squirrels*

SPECIES AND NUMBER OF STOMACHS	PERIOD	SEED	FUNGUS	LEAF	FLOWER	FRUIT	ROOT	ARTHROPODS	FLESH
C. lateralis	Spring	3	29	56	9	tr.	1	1	1
		(9)	(53)	(88)	(14)	(1)	(3)	(4)	(1)
273	Summer	6	65	7	1	1	2	16	2
		(14)	(81)	(30)	(4)	(1)	(4)	(25)	(4)
	Fall	4	90	2				1	3
		(12)	(100)	(14)				(5)	(5)
E. amoenus	Spring	35	12	17	7	tr.	1	27	tr.
		(61)	(20)	(41)	(16)	(1)	(1)	(52)	(1)
170	Summer	33	40	4	1			22	
		(55)	(58)	(16)	(3)			(50)	
	Fall	56	31					13	
		(71)	(52)					(40)	
E. speciosus	Spring	18	8	3	61			10	
		(31)	(11)	(21)	(85)			(46)	
126	Summer	42	25			1		31	1
		(73)	(42)			(4)		(50)	(4)
	Fall	28	62		4			6	
		(42)	(73)		(4)			(25)	
E. townsendi	Spring	8	62	tr.	30			tr.	
		(14)	(86)	(7)	(57)			(7)	
48	Summer	8	66			5		21	
		(17)	(36)			(8)		(33)	
	Fall	8	89	tr.				3	
		(5)	(95)	(5)				(9)	
E. quadrimaculatus	Spring	17	34	22	11			15	1
		(28)	(59)	(44)	(18)			(38)	(14)
165	Summer	16	76	tr.		5		3	tr.
		(20)	(89)	(4)		(7)		(9)	(2)
	Fall	10	88	tr.				2	
		(23)	(97)	(4)				(3)	

In fall—a season of warm days, dusty soil, and tinder-dry litter—herbaceous vegetation disappeared; seed supply of whitethorn was exhausted; seeds crops of oaks and conifers failed for the second year in succession, with the exception of a few sugar pines; and hypogeous fungi attained maximum numbers.

Table 1 is a summary of percentage volume and percentage frequency of types of food in all stomachs examined during 1951. The records are segregated according to seasons, which are based on plant phenology at each collecting site. The summary helps to reveal important types of food, to indicate seasonal trends in their use, and to suggest differences in feeding habits. But, as stressed

by Martin, Zim, and Nelson (1951), there is danger of "attributing unwarranted finality or accuracy to the food-habits data as expressed in percentages." That statement is especially true when, as in this study, the percentages reflect unequal sampling of a variety of habitats.

SEED

The proportion of seed in the diet was surprisingly small. Had the 1950 seed crop of woody plants not failed (Jameson, 1952, 1953; Tevis, 1952), consumption during the following spring probably would have been greater. The reason is that at harvest time chipmunks bury seeds in innumerable places in the ground. Then in the spring after emerging from hibernation they seek their caches. Hence, failure of the autumnal seed supply means a scarcity of vernal food.

The earliest *E. quadrimaculatus* that I trapped had its cheek pouches crammed with nutlets of manzanita and its stomach with endosperm, all of which undoubtedly came from a cache. If not found, caches often sprout, which, in the case of coniferous seeds, may aid reforestation (Plate I). But when clumps of shrub seedlings (Plate I) appear after a forest has been swept by fire, it is apparent that through spreading seeds chipmunks contribute to the establishment of dense brushfields, which hinder the return of timber.

Ceanothus cordulatus and prostratus.—As a rule, mantled squirrels ate fewer seeds than chipmunks, but there were times when they took significant amounts. One of these was in late summer when the erect whitethorn and its mat-like relative, squaw carpet (*C. prostratus*), ripened a bumper crop that attracted both kinds of rodents. The agile chipmunks, climbed branches of the whitethorn to collect seeds, but the heavy-bodied squirrels stayed on the ground. Accordingly they ate seeds of squaw carpet only. On other occasions, too, I noted that ground squirrels avoided foods whose procurement involved arboreal acrobatics.

For a month and a half the seed of whitethorn was a major food of chipmunks. In one series of stomachs of *E. quadrimaculatus* it was present in every stomach and comprised 88 per cent of the volume of the total contents.

Arctostaphylos patula.—The seed of manzanita was of primary importance to the many individuals of *E. quadrimaculatus* living in or about Sierran brushfields. Failure of the crop two years in succession undoubtedly affected the chipmunks. In 1950, flowers were killed by a late frost; in 1951, a gall-forming aphid [*Tamalia coweni* (Cockerell)] attacked fruits throughout the range of *E. quadrimaculatus*. By late summer, the berries were lumpy, blotched red, and in place of seeds contained cavities jammed with aphids.

Manzanita seed was eaten also by the other species of chipmunks but not by the mantled squirrel.

Collinsia parviflora.—A small figwort abounding in some dry, open places occupied mainly by *E. amoenus* and the mantled squirrel was one of the earliest forbs to ripen copious amounts of seed. During late spring, when it occurred in every stomach of *E. amoenus* examined and accounted for 70 per cent of total volume of the contents, many individuals of that species seemed to depend upon it, and aggregations of the chipmunks were centered in areas of *Collinsia*. Chipmunks ate the seeds after delicately extracting them from pods, but mantled squirrels obtained them incidentally while devouring the whole plants.

Conifers.—During some years coniferous seedlings sprout so thickly on the forest floor as to appear like a lawn. In 1951, I did not find one seedling. Probably rodents had taken the few seeds produced the previous fall. But I have no direct evidence of the quantity of coniferous seeds that are destroyed by chipmunks and squirrels when the supply is plentiful.

Unexpectedly, I failed to find a significant amount in stomachs of animals trapped under a few productive sugar pines. One reason was that the chipmunks generally cached the seeds.

I suspect that where hypogeous fungi are common, mantled squirrels consume relatively few seeds of conifers. One individual disregarded sugar pine cones cut by a chickaree. Instead, making frequent trips away from its feeding station, it returned each time with a fungus. Also, captive squirrels refused to extract seeds from closed cones of sugar pine until

denied all other food. They were apparently reluctant to undertake the labor of cutting off the bracts.

A serious charge against the chipmunk is that it selects seeds of commercially valuable pines and Douglas fir in preference to those of the inferior white fir and incense cedar (Horn, 1938; Krauch, 1945). Individuals of *E. quadrimaculatus* and *E. amoenus* that I kept in cages refused to eat seeds of cedar and white fir, but relished pine; and ones of *E. townsendi*

PLATE I

Upper Left. A cluster of sugar pines that sprouted from a rodent cache. Plumas National Forest, California. August 21, 1951. Upper Right. A cluster of 112 manzanita seedlings that sprouted from a rodent cache after a forest fire. Stanislaus National Forest, California. April 27, 1951.

Lower Left. Pits dug by mantled squirrels searching for hypogeous fungi. Sierra National Forest, California. June 5, 1951. Lower Right. Flowers of manzanita left by chipmunks on a stump. Lassen National Forest, California. May 7, 1951.

trapped under an incense cedar from which a chickaree was dropping ripe cones had empty cheek pouches and only fungus in their stomachs. Apparently, then, a high population of chipmunks is likely to encourage reforestation by white fir and incense cedar at the expense of pines and Douglas fir.

FUNGUS

Hypogeous fungus, which rodents obtain by digging, is the most important food of chipmunks and mantled squirrels in the commercial timber belt of northeastern California.

Were it not for the presence in the soil of this nutritious food, numbers of diurnal rodents now swarming over many areas would be sharply reduced.

Fungi occurred in stomachs throughout the year, as shown by Table 1 (the figures in the fungus column refer almost entirely to hypogeous forms, except for a few surface kinds which were taken in the spring). Often the first animals to emerge from hibernation found little to eat except "truffles", which presumably had survived from the crop of the previous fall. In one area, 66 per cent of the total volume of stomach contents of the earliest mantled squirrels consisted of hypogeous fungi, but two weeks later when forbs and grasses sprouted, the animals switched to eating green vegetation.

Because of their subterranean location, hypogeous fungi were well adapted to the long dry season of California and are able to attain maximum numbers in the warm autumn. As to be expected, therefore, consumption of them by animals shows a seasonal rise from spring to fall. But even in May, pits left by "truffle"-digging rodents were common (Plate I), and by mid-June *E. townsendi* and *quadrimaculatus* of certain habitats ate hypogeous fungi almost to the exclusion of everything else. The seasonal trend was most pronounced among squirrels, whose largest populations occurred only in areas of abundant "truffles" and least marked among the seed and insect-eating *E. amoenus*.

A volcanic forest swarming with mantled squirrels during the hot, dry fall of 1951 demonstrated the dependence of rodents upon this food. The forest floor was dusty-dry and devoid of the herbaceous vegetation of spring; the heavy crops of *Ceanothus* seeds and fruits of gooseberry were exhausted; conifers and manzanita had failed to set seeds; wind insects were rare. To an observer unaware of the significance of innumerable small pits in the ground, food for rodents would have appeared non-existent and high numbers of animals a paradox. The answer was that every rodent had its stomach packed with hypogeous fungi.

Apparently the coniferous forests of the Volcanic Plateau and Sierra Nevada support not only quantities of underground fungi but also a variety of kinds. In rodent stomachs the color of the fungi may be coal-black, gray, brown, white, orange, greenish, or purplish, and the consistency firm, soft, fluid, or gelatinous. For centuries the Old World has produced truffles for human consumption, but in the United States, although $100,000 worth of the fungi are imported annually, and sold at five dollars per seven-ounce tin (New Yorker, December 15, 1951), no effort has been made to utilize this tasty produce of our forests.

Other forest rodents, besides the above-mantioned chipmunks and squirrels, which I have found to feast on "truffles" include *Citellus beecheyi*, *Tamiasciurus douglasi*, *Sciurus griseus*, *Glaucomys sabrinus*, *Neotoma cinerea*, and *Peromyscus boylei*. Further information about the use of this food was given in an earlier paper (Tevis, 1952).

LEAF

Grasses and forbs were the principal spring food of mantled squirrels. Some of the earliest individuals to awaken from hibernation had difficulty in finding sufficient leaf, but from the time seedlings appeared until the plants reached maturity, squirrels cropped the green cover voraciously. Between mid-March and April 1, "leaf" changed from 33 per cent to 95 per cent of the total volume of stomach contents. Later when vegetation matured and dried, there was an abrupt decrease in consumption. The insignificant amount taken during late summer and fall came almost entirely from woody plants.

Chipmunks, which are not leaf-eaters, took green vegetation only when forced to do so by scarcity of other food. In one area during early spring, "leaf" constituted 51 per cent of total volume of stomach contents of *E. quadrimaculatus*. But a month later when other foods were available, the figure dropped to zero despite a lush growth of grasses and forbs.

FLOWER

The importance of flowers has not always been appreciated by students of mammalian feeding habits. Flowers are not necessarily an incidental food; often they are a major component of the diet.

During the spring of 1951 when manzanita was loaded with bloom, the stomachs of nearly

all chipmunks from brushy areas were distended with a sweet-smelling pinkish mass containing the purple anthers of manzanita, and stumps were littered with pedicels stripped of their flowers (Plate I). Even mantled squirrels ate less herbage to take advantage of this suddenly available food. The scats of black bear (*Ursus americanus*) were composed of the remains of the flowers.

In Table 1, the apparent greater importance of flowers to *E. speciosus* is misleading. It is due to trapping a disproportionate number of those animals at the height of the blooming period. Other evidence indicated that manzanita flowers were equally important to *E. townsendi* and *quadrimaculatus*, but possibly less so to *amoenus*.

Although whitethorn bloomed profusely, little was eaten. Apparently there is a difference in palatability between the flowers of the two shrubs. In this connection it should be noted that chipmunks live in brushfields of pure manzanita but not in those of whitethorn.

A few stomachs of *E. speciosus* and *townsendi* contained pollen of white fir (*Abies concolor*) during the period of anthesis in May, and again when the old cones fell to the ground during the autumn. Feces of animals which ate staminate cones were golden in color.

FRUIT

Table 1 does not give an accurate picture of the proportion of fruit in the summer diet of chipmunks, for the least amount of trapping was done at the time of maximum fruiting.

I have records of *E. speciosus* eating manzanita berries and strawberries (*Fragaria californica*). But the fruit which appeared to be most relished by chipmunks, although not taken by the mantled squirrel, was Sierra gooseberry (*Ribes roezli*). In the late fall of 1951, bushes were heavily loaded with fruit.

Stomachs of gooseberry-eating *E. quadrimaculatus* contained pulp and whole seeds but no spines or skin. Although chipmunks masticated seeds of manzanita, whitethorn, fogwort, etc., gooseberry seeds taken incidentally with the pulp were not injured. Presumably they remained viable, for Krefting and Roe (1949) showed that rodents assist the dispersal of some plants by defecating germinable seeds.

Spreading gooseberry makes the chipmunk an ally of blister rust and an enemy of man in his costly effort to control the "scourge of sugar pine". The only known method of checking the disease is to destroy all the current and gooseberry bushes in and near forests that contain any of the white pines—a large and difficult undertaking." (Betts, 1945.)

Another woody-plant having an abundant fruiting year was bitter cherry (*Prunus emarginata*), but I found no evidence that it was utilized by rodents.

ROOT

Bulbs and roots were of little consequence in the diet. It is probable, though, that because of their digging habits mantled squirrels ate more than chipmunks. One squirrel stomach contained nothing but wild onion (*Allium*).

ARTHROPODS

Only during outbreaks did squirrels and chipmunks (except *E. amoenus*) capture large quantities of insects. As evidence of this, the mantled squirrel is not usually an insect-eater, but when there was an outbreak of larvae of the tortoise-shell butterfly, 60 per cent of the total volume of the contents of a series of stomachs of this rodent was composed of caterpillars. After the outbreak subsided, fungus again became the chief food.

Foresters are interested in knowing if rodents can check outbreaks of insect enemies of the forest. Perhaps the most clear-cut example of effective predation under certain conditions is the explanation by Bess, Spurr, and Littlefield (1947) of why New England's gypsy moth (*Porthetria dispar*) defoliated trees in some regions but not in others. Predators of the forest floor, including small mammals, were effective control agents in mesophytic woodlands, where the caterpillars rested in ground litter, but they were not effective under xeric conditions that restricted the larvae to tree tops.

Nymphalis californica (Bdv.).—According to Keen (1939), "The California tortoise-shell

butterfly . . . often appears in such numbers as to attract public attention. The caterpillars feed on different species of *Ceanothus*." During early July, 1951, a severe outbreak occurred at Lake Almanor, twenty miles northwest of Quincy. By the middle of the month whitethorn was defoliated. Then the larvae deserted the naked shrubs and migrated across ground to the undersides of white fir boughs, where they pupated. En route they were attacked by mantled squirrels. The rodent population was high.

Since whitethorn regained its foliage within a month and chrysalids did not affect conifers, the outbreak had little economic interest. But it provided clues as to possible efficacy of chipmunks and squirrels to stop serious pests, such as the pine butterfly (*Neophesia monapia*), which, in Idaho, defoliated ponderosa pine over thousands of acres, killing a quarter of the trees and stunting the remainder (Evenden, 1943).

At Lake Almanor, the mantled squirrel fed extensively on the caterpillars they captured on the ground, but chipmunks, apparently repelled by the bristles on the larvae, ate mainly chrysalids. *E. amoenus* took almost no other food during the height of the pupation period. The other three species ate lesser amounts.

After hatching, butterflies swarmed onto the forest, and clouds of them drifted with the air currents even up to and over the summit of nearby Lassen Peak, a volcanic crater rising more than ten thousand feet above sea level. This winged invasion of Lassen National Park from the Almanor region was one of the largest on record. Hence, rodents did not check a major outbreak of the tortoise-shell butterfly. A reason for their ineffectiveness was lateness of the attack. Squirrels did not capture caterpillars until the latter marched from the bushes, and chipmunks waited until the larvae transformed into chrysalids. In the case of control of an ethmiid moth by chipmunks (Tevis, 1952) and in the example of New England's gypsy moth, predation was effective because it began with the larvae.

No blanket statement can be made that small mammals do or do not check outbreaks of insect enemies of the forest. No two situations are alike. But sometimes through knowledge of feeding habits, man can enlist the aid of rodents. Rust (1935) believed that at least on one occasion small mammals and other predators accounted for success of the bark-peeling technique of destroying the mountain pine beetle (*Dendroctonus monticolae*).

Chermes pinicorticis Fitch.—Chipmunks, but not squirrels, ate aphids that, for about a month (June–July), infested young needles of white fir throughout the Volcanic Plateau and Sierra Nevada. The maximum consumption recorded at any one time was 64 per cent of the total volume of a series of stomachs of *E. speciosus*. The insects were swallowed whole, and often bits of needles were included. Twelve years earlier, Baysinger (1940) had observed chipmunks feeding on white fir aphids in Yosemite National Park.

Zootermopsis angusticollis (Hagen).—A while on a particular quiet, sultry afternoon in mid-May there did not seem to be a chipmunk in the woods. Then shortly before sundown the forest became alive with the wing-rattling of termites streaming from slit-like holes in damp logs and taking to flight. Almost at once, chipmunks (*E. quadrimaculatus*) appeared. Excitedly they ran from hole to hole to grab the insects popping out. A chipmunk devoured one of every twenty termites that emerged from a log. But since the number of colonies greatly exceeded the number of rodents, the effect on the swarm was negligible.

Reticulitermes hesperus Banks.—The stomach of an *E. amoenus* contained innumerable subterranean termites, which apparently had been obtained by digging.

Unidentified pupae.—Bits of reddish bark from trunks of ponderosa pine occurred in stomachs of *E. quadrimaculatus* that had eaten unidentified pupae and eggs.

Lepidopterous larvae.—*E. amoenus* often searched for insects. During March even before leafing of bushes, stomachs of animals living in a cherry thicket were filled with a species of lepidopterous larva occurring sparsely in litter of old leaves.

Camponotus levigatus (F. Smith).—Insignificant amounts of the giant carpenter ant, which wandered singly over the forest floor, showed up in rodent stomachs of all species studied except *E. amoenus*. Always the victims were decapitated and the heads discarded. But a tiny amber-colored ant, taken by *E. amoenus* as well as by other chipmunks, was swallowed whole. A wolf spider provided a little food, but, in the main, neither spiders nor ants

were relished. At times they could have been captured in large numbers, yet they never constituted more than ten per cent of the contents of a stomach.

FLESH

Often when specimens in traps had been mutilated, I found flesh in stomachs of other animals caught afterwards. Mantled squirrels were more carnivorous than chipmunks, but the degree of cannibalism varied with locality. One squirrel stomach contained a lizard (*Sceloporous gracilis*) and five of its eggs. A sixth egg was in a cheek pouch. Each of two other stomachs contained feathers and flesh of junco (*Junco oreganus*). An *E. quadrimaculatus* ate a garter snake (*Thamnophis ordinoides*) crushed by an automobile.

COMPARISONS

Because of its capacious stomach and caecum, the mantled squirrel endeavored to consume massive amounts of food, a trait which contrasted with the fastidious habits of chipmunks. Essentially the squirrel was a gross feeder in open or semi-open areas, cropping herbaceous vegetation during spring and digging hypogeous fungi for the remainder of the season. It did not search litter for individual insects; it took only those that appeared *en masse*. It did not climb trees or shrubs; it gathered only seeds that were both sizeable and available at ground level. It ate fewer flowers than the chipmunks, and depended less on seed caches.

Although the differences between feeding habits of squirrels and chipmunks are apparent whenever investigated in a single habitat, the differences within the chipmunk group are less easy to detect. One generality, however, applies to all kinds studied: the larger the species the greater the proportion of fungi and the smaller the proportion of seed and insects in the diet. Table 1 shows the extent of this correlation. The squirrel is larger than any chipmunk, *E. townsendi* and *quadrimaculatus* are next in size, *speciosus* is intermediate, and *amoenus* is smallest.

A single insect captured after a diligent search through litter or tiny seeds extracted from a pod might fill a significant portion of the stomach of an *E. amoenus* but would not begin to fufill the needs of a squirrel. The latter could use the same period of time more profitably by cropping massive amounts of vegetation or by digging for hypogeous fungi, one of which might constitute a full meal. Also, a small animal can poke more efficiently into places where insects hide, and a large animal can be more effective in digging.

CONCLUSIONS

From the standpoint of forestry, the chief conclusion that derives from this study of feeding habits is the impracticality of assigning each species of rodent an economic rating. Interrelations within the forest are too complex and changeable. A species that is harmful at one place or at one time may be beneficial nearby or later in the season or at the same time another year. A better approach to an evaluation of the rodent factor in forest ecology is Duncan Dunning's philosophy of silviculture: every area with its plants and animals should be studied and managed as a unit unto itself.

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ENVIRONMENT OF THE NELSON ANTELOPE GROUND SQUIRREL

BY ALBERT C. HAWBECKER

A study of the Nelson antelope ground squirrel (*Ammospermophilus nelsoni*) was started in 1940 when an investigation into its food habits was undertaken. This study has been published (Hawbecker, 1947), and since that time other phases of the life history of the squirrel have been investigated. The present paper deals with the factors most pertinent to the environment and specific habitat of the squirrel. The northern part of the range has been studied most intensively, with most of the work being done in three areas. These have been described in the above-mentioned paper and need not be repeated here. The southern part of the range has been worked through also in this study, but many of the data for that area have been taken from the works of Grinnell and Dixon (1918), who worked in the southern part of the range, and from Piemeisel and Lawson (1937). Many of the records are from the collections of the Museum of Vertebrate Zoology, University of California, and have been made available by Dr. Alden H. Miller. The maps are the work of Mr. George C. Jensen.

RANGE

The extent of the range of this squirrel is best understood by studying the accompanying maps which are adapted, in great part, from Piemeisel and Lawson (*op. cit.*). Here it is seen

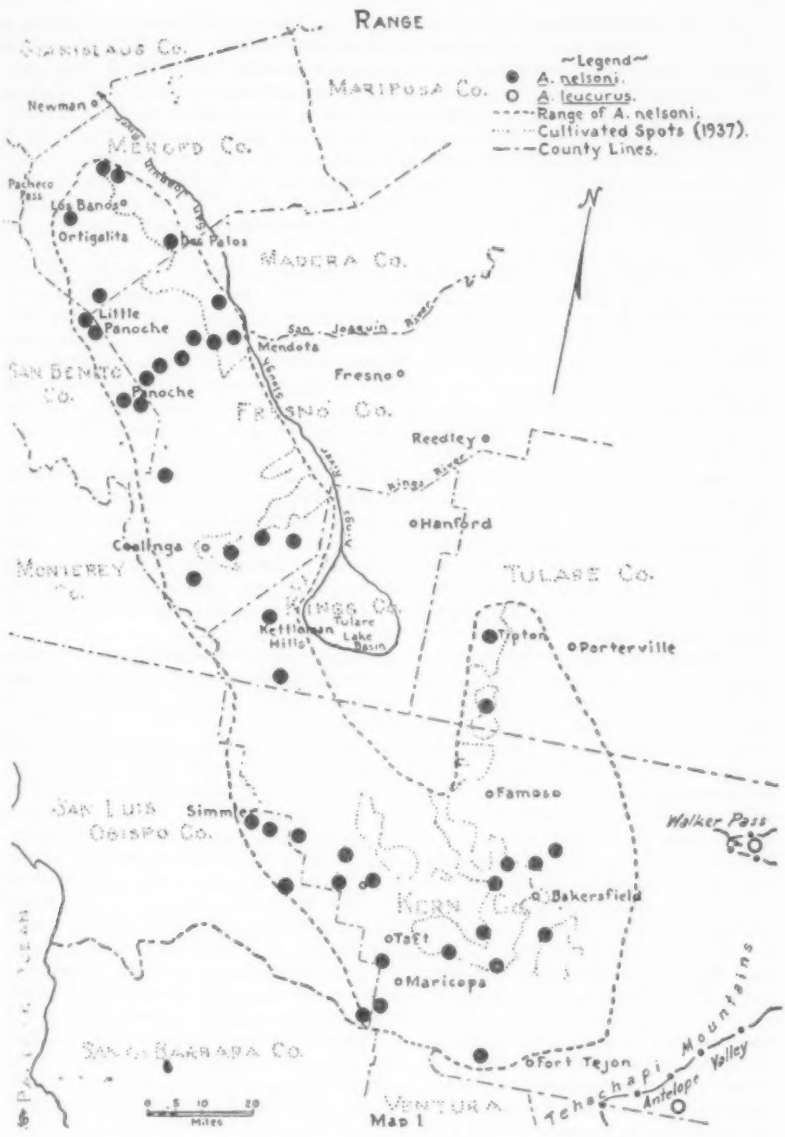

FIG. 1.—Map showing range of Nelson antelope ground squirrel.

that the present range lies completely within the limits of the west-central and southern San Joaquin Valley and adjacent foothills. It is the purpose of this section of the paper to consider the factors that limit the range.

It would appear that the original invasion of this area by antelope ground squirrels, as well as by the ancestors of such present plants as desert saltbush (*Atriplex polycarpa*) and ephedra (*Ephedra californica*) has been over the comparatively low passes of the southern Sierra Nevada and the Tehachapi Mountains. The best evidence for this is that the nearest present-day relatives of these organisms are just across these passes in the Mohave and adjacent desert areas. At present the ranges of the Nelson antelope ground squirrel and its nearest relative, the white-tailed antelope ground squirrel (*Ammospermophilus leucurus*) are only narrowly separated, as the latter is found just across the Tehachapi Mountains in Antelope Valley and in Walker Pass in the Sierra Nevada (Fig. 1). Changes in climate since the invasion, or a further uplift in the Tehachapi Mountains, may account for the lack of squirrels in the passes today.

After coming into the San Joaquin Valley the squirrels and the saltbush have spread all across the southern portion of the valley and the foothills, as well as to the smaller adjacent valleys. Expansion northward has been somewhat restricted, as the squirrel has been found only as far north as Tipton, Tulare County, on the east side of the valley, and Los Banos, Merced County, on the west side. It is relatively easy to assume that the squirrels have not spread further west, south, or east because here they encounter steep, wooded hills, and a study of their habits shows that such areas are usually avoided. What prevents them from invading the open land to the northwest is not so clear. Possible factors limiting this movement are discussed in the following paragraphs.

A study of the food habits (Hawbecker, 1947) indicates that red-stemmed filaree (*Erodium cicutarium*) and red brome (*Bromus rubens*) are the most important items in the diet of the squirrel. There is much evidence that the squirrel is very omnivorous, as vegetable and animal food of many types are taken, which might indicate that lack of a particular food item, or even group of items, would not prevent its existence or spread. Certainly, its two main food items extend much further to the northwest than does the squirrel. Thus there is little evidence that the squirrel is prevented from extending its range northward by the lack of suitable food.

A second factor possibly involved is the apparent dependence of the squirrel on widely spaced shrubby vegetation. A study of the squirrel throughout its range during the breeding season shows that the burrows most used, whether original breeding burrows or not, by adult females and their newly-emergent young, are burrows under some shrub, such as ephedra or desert saltbush. Females with young, though present, were found with difficulty in such areas as Ortigalita Canyon, where brushy cover was absent. Much brushless land was investigated during the breeding season, but squirrels were found in only a few places, and then seldom in a breeding condition. Squirrels are occasionally found in such places, but they may be the more "venturesome" ones found along the edges of any population. South of Panoche, where the hills are more commonly covered with desert saltbush, squirrels with young were relatively easy to find. This shrub is found to extend north and west almost as far as the present records for the squirrel (Fig. 2). Local patches of ephedra harbor squirrels where the saltbush is absent, and these patches account for many of those records for the squirrel outside of the range of the saltbush (Fig. 2). Other factors must be emphasized. Squirrels of this species are not normally found on steep slopes even though scattered shrubs are present; also, close spacing of shrubs keeps out the squirrels. Grinnell and Dixon (1918), who studied the squirrel in the southern part of its range, always associated it with desert saltbush or rough, dry washes. In the more northerly part of its range *A. nelsoni* is associated with *Ephedra* in addition to the two habitats mentioned by Grinnell and Dixon. The few rock outcrops present may also be used. The habitat of the spiny saltbush (*Atriplex spinifera*) is invaded but sparingly, as it is usually found in alkali and such soils appear to be avoided by the squirrel.

A third major factor that must be considered in discussing the distribution of this squirrel is soil type. This may be an indirect factor, as will be pointed out later, but, even so, the relation between soil distribution and range of the squirrel is apparent. The soil types on which the antelope ground squirrel is found almost exclusively, are Panoche (soil outlined on Figure 3), Kettleman, and Fresno loams and sandy loams, in that order. Soils derived

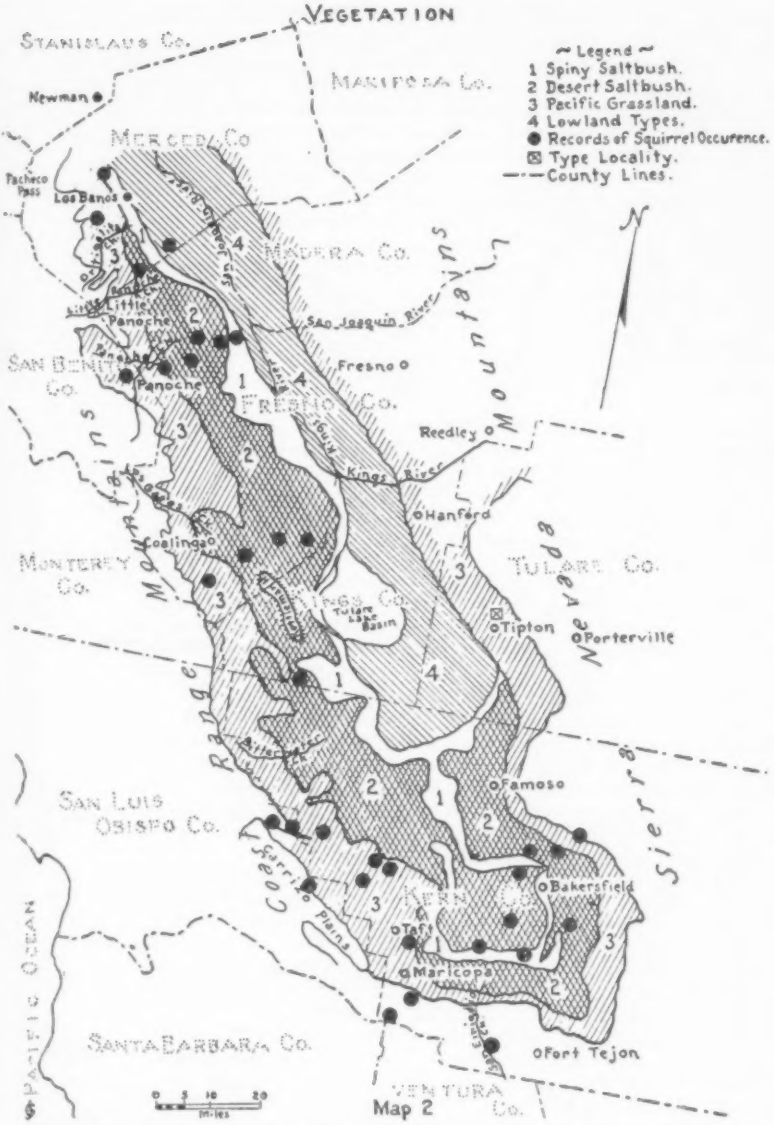

FIG. 2.—Types of vegetation within the environment of the Nelson antelope ground squirrel.

from sedimentary rocks are favored, and of these the Panoche series is by far the most acceptable. Nowhere is the squirrel found, other than just a straggler, where alkali is abun-

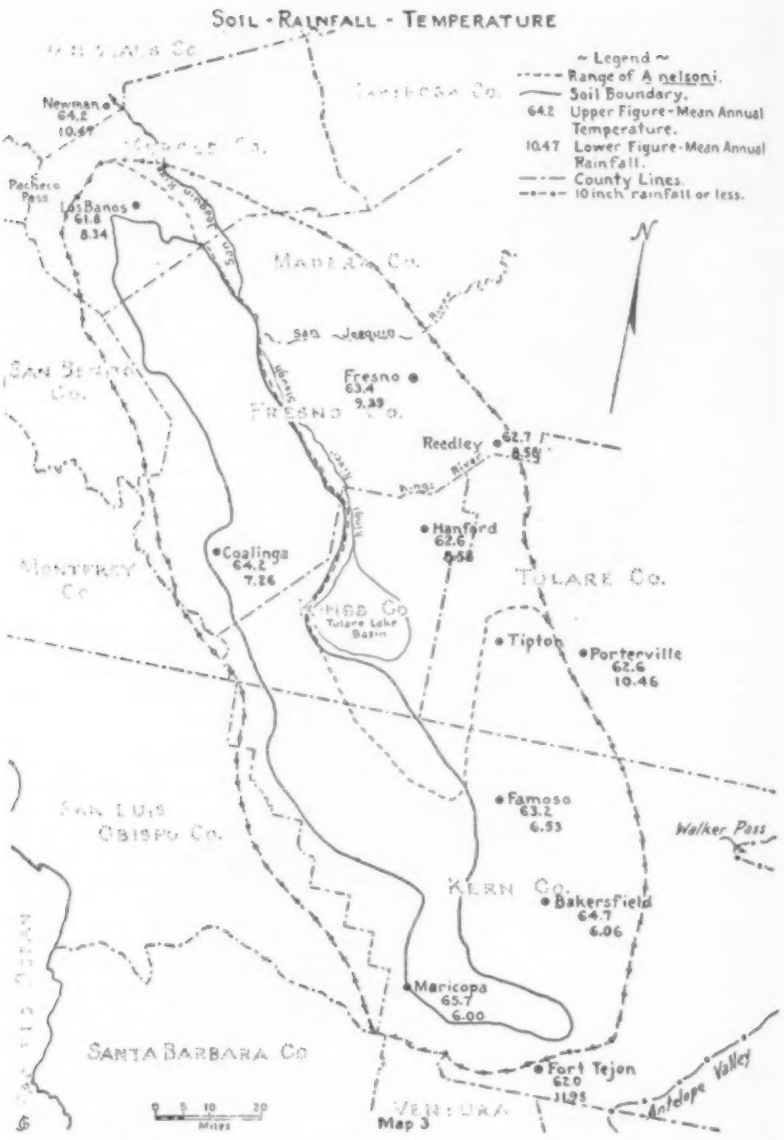

FIG. 3.—Soil, rainfall, and temperature in the environment of the Nelson antelope ground squirrel.

dant. Panoche loam, the soil where most of the squirrels are found, is "derived from recent alluvial deposits of gray or light-gray to light brownish-gray color and coming principally

from sedimentary rocks. The soils are low in organic-matter content. . . . Hardpan or dense subsoils are not typically present. These soils occupy broad alluvial fans and alluvial valley slopes and small areas of stream terrace and stream bottom" (Holmes, et al, 1919). Soils on the east side of the valley are derived from metamorphic rocks and are higher in organic content. Whether there is some characteristic of these types of soils that prevents the antelope ground squirrel from inhabiting them is not known. It does not prevent the California ground squirrel (*Citellus beecheyi*) from living in them. The soils of the Panoche series are usually well drained and are "diggable" in both wet and dry weather—that is, they do not become too hard in the summer or too wet and sticky in the winter. The California ground squirrel may be found on the same series, but is in no way limited by it. Grinnell and Dixon, in their study in the southern part of the range, found that this soil type seemed essential to the habitat of the antelope ground squirrel. As these squirrels are found in the better soils—alkali-free loams and sandy loams—they are being crowded out as these fertile soils go under cultivation. Figure 1 shows cultivated areas in 1937 in relation to squirrel distribution, and much more land is under cultivation now. Only those parts of the range that are not potentially irrigable or cultivatable appear to be safe for the squirrel. It can maintain itself on pasture land, but not, as can the California ground squirrel, on irrigated or cultivated land.

This affinity for alluvial and loamy soils may not be due to the digging habits of the squirrel itself. Repeated excavation of burrows in which squirrels were noted revealed that seldom, if ever, did the squirrel occupy burrows dug by itself. All evidence of construction and appearance indicated that the antelope ground squirrel utilized burrows dug by kangaroo rats. Thus, one of the factors involved in the spread of the squirrel in a northerly direction might be the spread of other animals that the squirrel depends on for burrows. A study of the range of the Tulare kangaroo rat (*Dipodomys heermanni tularensis*) by Grinnell (1922) shows that the range of this animal not only includes, but also extends beyond the range of the squirrel. The range of the giant kangaroo rat (*Dipodomys ingens*), as delineated by Grinnell (*op. cit.*), is included within the range of the squirrel but is not as extensive. It appears, however, that even though the burrows of these two species are used, the squirrel is not entirely limited by them, but by some other factor or factors.

A fourth factor, obviously the one upon which the others depend, that may affect the ground squirrel directly is climate. A study of two climatic constituents, heat and rainfall, using data from the Weather Bureau (1947) publications, shows that there is a gradual decrease in mean annual temperature and increase in mean annual rainfall as the northwestern end of the range is approached (Fig. 3). Special note should be taken of the abrupt change between Los Banos, Merced County, and Newman, Stanislaus County. Here, within 20 miles, there is a change of 2.13 inches in rainfall. This is taken from cumulative records, and the variation may be much more, or much less, from year to year. There is here, then, a change from desert to non-desert conditions. Piemeisel and Lawson attribute this sudden change to the influence of the break in the Coast Range at the level of San Francisco Bay. They suggest that this change has inhibited the northern spread of desert and spiny saltbush. This increase in rainfall, and possible increase in humidity, may also be responsible for the limitation of the range of the ground squirrel. It can be seen, by referring to Figure 3, that nowhere is the squirrel found where the rainfall reaches nine inches. Significantly, the ranges of the desert species of plants and many of the associated animals, such as the giant kangaroo rat and *Dipodomys nitratoides*, also lie within this boundary. Thus, this ground squirrel may be limited to desert conditions. There appears to be less of a tie-in with temperature, as adjacent areas of like temperatures have not been invaded. The nearest area of like precipitation is across the Sierra Nevada-Tehachapi chain, where the white-tailed antelope ground squirrel is found (compare Figs. 1 and 3).

RESPONSE TO WEATHER CONDITIONS

Weather, as would be expected, plays a very important role in the seasonal and daily activities of the animal. Just how important this is in limiting the range is not clear, but the effect on the amount of foraging time available during the winter period might have an

effect on the range. Many winter days (81) spent in the western hills along the San Joaquin Valley have shown that there is more winter fog north of the Los Banos region than south of it. This lack of sun, added to the already cold winter days, may have something to do with the reduction of the length of the winter daily, as well as seasonal, feeding period. This shortened feeding period could limit the spread of the squirrel to the northward. To test the sensitiveness of the squirrel to changes in weather conditions, observations were made month by month and year by year. In the following discussion, such humanly interpretable terms as "pleasant", "cool", "warm", and "hot" can be applied, as it was found early in the study that these squirrels would be out and active when conditions were pleasant from a human viewpoint, and would be inactive when conditions were considered as rigorous. Actual temperature might not always be a factor, but repeated tests showed generally that squirrels were not out when a thermometer, laid on the ground, registered more than 90°F. or less than 50°. It was noted that the days and hours the squirrels would be out depended on weather conditions, and bore little relation, other than in a general way, to the month of the year. October 11, 1940, was a very hot day, and it was impossible to find any squirrels out until evening. October 14 and 15, 1944, were pleasantly cool days and squirrels were seen out between dawn and dusk in abundance. November 5, 1940, was a pleasant day, and squirrels were encountered all day, but the same date in 1942 was cold and cloudy, and very few squirrels could be found anywhere. November 29, 1946, was pleasantly warm in the middle of the day, and squirrels were much more in evidence during that period. December 11, 1940, was a pleasant day and squirrels were noted as common all day. December 21, 1942, was cold and foggy and squirrels were out only in the period around noon. January was uniformly cold during all of the observation periods, and squirrels were out only near the middle of the day, which was usually the least cold part. February followed much the same pattern, except February 16, 1942, which was clear and warm, and many squirrels were noted out most of the day. March was also quite cold, but the days began to warm up near the end of the month and squirrels spent more and more time out. April showed the reverse of the winter period, with the days becoming hot and the squirrels coming out in the morning and evening only. From May until October the early and late periods of the day were used in gleaning food. One incident on May 19, 1942, indicates the effects of heat on this species of squirrel. Three squirrels that had been kept captive for several months were released in a slightly different spot from that in which they had been taken. It was very hot and there was no shelter other than strange burrows. Two squirrels ran into the shade of the car, one even leaping up into the motor compartment. The third took refuge in my shadow and followed that shadow wherever it moved. It appeared much more affected by the direct rays of the hot sun than it did by my presence. It was noted that California ground squirrels were out feeding at this time, and showed little regard for the heat. The examples of monthly and daily activity quoted above are only a few from a long list of similar records.

It can be seen that during the cold periods of the year mid-day is utilized for aboveground activities, and during the warm periods the early morning and late afternoon hours are used. There seems, under the latter condition, to be an emphasis on the use of the morning period. Such days as the above are characterized by intensive feeding with very little moving about. The point seems to be to get as much food as possible and then get back down out of the heat or cold. Days of moderate temperatures are favored, and, during such days, feeding and other aboveground activities are carried on in a more leisurely fashion. The squirrel may stay out all day with only very short periods beneath ground, and, in the course of a day, a circuit of hundreds of yards may be made. The pleasant days of late winter and early spring are utilized for the breeding period, when the maximum amount of green food is also present. Cloudy days are not favored and days lacking sunshine are avoided wherever possible. Wind is not tolerated except on warm days, when necessary surface feeding is made more bearable by the breeze.

Rain appears to have less of an effect on these squirrels than might be expected. On days after a rain, while the ground was still wet, squirrels were not seen out in large numbers. Cold and wet mornings, in particular, seemed to be avoided. Squirrels were seen to disap-

pear during a hard shower, but, if the sun came out following this, they would soon reappear. December 27, 1945, was rainy all day, and the several previous days had had some rain. Four squirrels were seen working in the light rain, showing no hurry but working as on a moderate day. This day was not cold, however. Thus rain, unless it is too intense or the ground is too wet and cold, does not seem to be an important factor in the above-ground activities of the squirrel.

ASSOCIATED ANIMALS AND ENEMIES

Living in relatively the same habitat, though not necessarily restricted by the same factors, are a number of other animals that in many instances affect, or are affected by, the Nelson antelope ground squirrel. Shaw (1934), Grinnell (1932), and Hawbecker (1951) discuss some of the animal relationships of this area, but in general the ecology of this interesting community has been left untouched. It will be impossible to discuss all of the interrelationships, even between the squirrel and other mammals, so only those that appear most significant will be listed.

The June beetle (*Phyllophaga errans*), valley grasshopper (*Oedaleonotus enigma*), camel cricket (*Ceuthophilus californicus*), and the Jerusalem cricket (*Stenopelmatus longispina*) figure prominently in the diet of the squirrel when and where available (Hawbecker, 1947). The harvester ant (*Pogomyrmex*) has been found in squirrel stomachs, particularly when other insects are not available. The tumble bug (*Eleodes*), though the commonest large insect present the year around, has never been found to be utilized in any way. The tarantula (*Eurypelma californica*), black widow (*Latrodectes mactans*), northern scorpion (*Vejovis boreas*), and the camel cricket are usually found inhabiting the burrows the squirrels use for refuge. It is apparent, however, that they are not numerous in well-used, well-kept burrows, but only in those that are abandoned, or used only occasionally. There is, as yet, no evidence that there is any closer contact than this between the arachnids and the squirrel.

The gopher snake (*Pituophis catenifer*) has been found but three times, by me, within the range of the squirrel. There was no evidence that the squirrel was taken, even though in these three instances the snakes were within a large colony of squirrels. These instances are far too few to judge the effects of this snake on the squirrel. The rattlesnake (*Crotalus viridis*) was found but four times, and, here too, there was no evidence that the squirrel was taken. Snakes have very seldom been seen in the locality during the 12 years of this study, so it may be that there are factors that limit the number of snakes. At any rate the squirrel is seldom bothered by these reptiles. The blue-bellied swift (*Sceloporus occidentalis*) is the most common reptile seen in this area, but it has been seldom found as a food item in the stomach of the squirrel.

Grinnell and Dixon (1918) indicate that squirrels seemed to have very little fear of the golden eagle (*Aquila chrysaetos*), but hurried to their holes when the red-tailed hawk (*Buteo borealis*) appeared. Neither bird was ever seen to make a capture, but a pellet from a red-tailed hawk was picked up that contained fur that was undoubtedly from an antelope ground squirrel. A study of pellets from beneath barn owl (*Tyto alba*) nests (Hawbecker, 1945) showed no antelope ground squirrel remains. Tappe (1941) found one instance of the squirrel, in the same general area, from pellets picked up under the nest of a horned owl (*Bubo virginianus*). Casual observation and pellet examination of the burrowing owl (*Speotyto cunicularis*) gave no indication that this owl preyed upon even the young. So few records of these squirrels in the pellets of owls is probably due to the foraging of the owls at night, for these ground squirrels have never been seen out even in the late dusk.

The horned lark (*Otocoris alpestris*) both feeds and nests on the ground, and many instances of meetings between this bird and the squirrel have been recorded. During the nesting season the birds are seen to chase and pick at the squirrels, so it is possible that the squirrels bother the nests. Of greater significance is the fact that this bird, as well as the white-crowned sparrow (*Zonotrichia leucophrys*), serve as "lookouts" for the squirrel. When the birds are disturbed and give out their alarm notes, the squirrels give close attention for a moment. If the squirrel is on guard the actions of the birds may stimulate it to dive down

a hole. It is impossible to stalk the squirrels when the birds are about. Chance meetings, other than in nesting season, result in the squirrel dashing at the bird and the latter flying away. No instance of capture was noted. A female squirrel, with young, was seen alone near a shrike's (*Lanius ludovicianus*) nest, and the bird was seen to dash out and chase the squirrel away. The young squirrels were never seen near the nest. Other shrikes were seen to chase squirrels, even when not nesting.

No actual attacks by weasels (*Mustela frenata*) on antelope ground squirrels have been observed, but in one spot, where a female weasel is known to have raised a family, live-trapping records have shown a decrease in the number of squirrels over the previous year. Many diggings of the badger (*Taxidea taxus*) have been noted in the past, but a predator campaign in the later years of the study appear to have reduced their numbers. Grinnell and Dixon (1918) say that the badger is an important enemy of this squirrel. It is interesting, however, that even though there has been a campaign under way that has lowered the population of badgers, the squirrel, on the basis of live-trapping records, has also decreased. Kit foxes (*Vulpes macrotis*) are seen on every trip into the area and appear quite common, even though exposed to the same predator campaign. A rather incomplete study (Hawbecker, 1943) of the scats of this animal found around a den in a colony of the squirrels shows no evidence that the squirrel is used for food. Grinnell, Dixon, and Linsdale (1937) report one instance of the kit fox taking an antelope ground squirrel. The foraging time of the kit fox does not correspond to that of the ground squirrel, so there would be little opportunity for predation. The results of the predator control campaign are systematically hung on a fence, and if this is any indication, the coyote (*Canis latrans*) is the most numerous predator in the area. Coyotes have been watched during the day on the study area, and scats have been examined, but there is no indication that the squirrel is preyed upon to a great extent. The wildcat (*Lynx rufus*) has been seen on the area, but there is no known record of its preying on this squirrel.

The California ground squirrel appears to be a competitor of the antelope ground squirrel under marginal conditions. Grinnell and Dixon show that they appear almost side by side and yet occupy slightly different habitats. Observations of my own have suggested both possibilities. Instances of close contact between the two species are quite common. In the Little Panoche and Ortigalita study area, during 1941 and 1942, both species could be collected from the same station by shooting. There were locations within these areas, however, where only a single species could be found. Work here in 1949 showed that in one location, formerly occupied by both, only antelope ground squirrels were found, and in another only California ground squirrels. These locations are considered, on the basis of comparison with locations where the most successful colonies are found, as marginal, and this may account for the finding of a species one time and not another. The most successful colony studied, to date, is the one in the Panoche area. Here no California ground squirrels were seen until 1948. Two of this species established themselves near the western end of the colony and were seen until 1950, when another was seen near the middle of the colony. In 1951, although the area was watched carefully, no California ground squirrels could be found. There have been few times when it has been possible to observe the two species together, yet it seems that some factor other than size must be at work. If size were all, the larger, seemingly more adaptive California ground squirrel would have "flooded out" the smaller, seemingly less adaptive antelope ground squirrel in the above-mentioned instance.

The influence of the kangaroo rats on this squirrel has already been discussed. There is some evidence that the squirrel will take over abandoned burrows, and in one instance a squirrel was seen to drive a kangaroo rat, of undetermined species, out of a burrow. Whether this indicates an actual taking over of a burrow is not known. Burrows used by the squirrel in setting up its feeding "beat" are almost invariably of kangaroo rat origin, but there is some evidence that brood burrows are not. There is little evidence that the two compete for food for, although they may use the same species of plants, there is always more seed than is utilized. The squirrels are out in the daytime and the kangaroo rats are out at night, so meeting above-ground is not a usual thing.

SUMMARY

The range of the Nelson antelope ground squirrel is limited, in the southern part of its range, by steep hills and arboreal vegetation. The reason for its restriction in the northern part is not clear; certainly it is not due to the lack of the accustomed food plants. A number of changes occur where its range stops which may, directly or indirectly, affect the squirrel. There is an increase in the mean annual rainfall and a greater incidence of winter fog; the soil type changes, which may also affect the kangaroo rats upon which the ground squirrel depends for burrows; and the widely spaced desert shrubs, often associated with the squirrel, disappear. Other desert species tend to disappear here also, indicating that what affects one affects the others. Every indication points to rainfall as being the limiting factor, for when the mean annual rainfall exceeds nine inches the above-mentioned changes take place.

This species is much more sensitive to weather conditions than is the California ground squirrel. Very warm days find *A. nelsoni* using the early morning and late afternoon to get food, while on very cold days it uses only the middle of the day. On pleasant days the squirrel is out most of the daylight hours, but it goes in when the sun goes down. Cloudy days are not favored, but rain does not necessarily keep the squirrels in.

The June beetle, valley grasshopper, camel cricket, Jerusalem cricket, and, more sparingly, the harvester ant, are found in the habitat of this squirrel and figure in its diet. None of the reptiles found on the area appears to affect the squirrel in any way as far as known. Raptorial birds, except possibly the red-tailed hawk, do not seem to catch the squirrel. The weasel appears to be the most serious predator on indirect evidence, although the badger may dig out the squirrels. The California ground squirrel occupies some of the habitat of the antelope ground squirrel. The relationship between the two has not been worked out, but an established antelope ground squirrel colony, in its own habitat, is able to withstand the encroachment of the larger squirrel. Along the edges of the habitat one squirrel may appear dominant at one time and the other species may appear dominant the following year. The most successful colonies appear to be those where there is one species exclusively. The kangaroo rats exert a great influence on the antelope ground squirrel, as their burrows are used by the latter almost to the exclusion of building any of their own. It seems possible that the range of the squirrel may be determined, at least to some degree, by the range of the kangaroo rats.

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A PRELIMINARY STUDY OF THE BARROW GROUND SQUIRREL, *CITELLUS PARRYI BARROWENSIS*

BY WILLIAM V. MAYER

This study, made possible by an Office of Naval Research Grant, was undertaken to provide information on the life history of the Barrow ground squirrel, *Citellus parryi barrowensis*, about which little has been recorded. The investigation was conducted at Point Barrow, Alaska, from July 12 to August 28, 1951, inclusive. This is contribution 1952–5 from work done partially at the Arctic Research Laboratory under Contract Nonr 377-(00) with the Office of Naval Research. Grateful acknowledgement is due Dr. Ira L. Wiggins, Director of the Arctic Research Laboratory, and to the laboratory staff, whose cooperation contributed much to the effectiveness of the project. Field work was carried out in three different localities of Naval Petroleum Reserve No. 4: (1) the vicinity of the Meade River, approximately 40 miles south of Point Barrow, July 17 to July 25; (2) an abandoned oil camp at East Oumalik, some 110 miles south of Point Barrow, July 31 to August 7; and (3) Teshekpuk Lake, about 115 miles east of Point Barrow, August 18 to August 24.

OBSERVATIONS

Distribution.—J. A. Allen (U. S. Surv. Geol. Territories, 1877) quotes Richardson on the distribution of the arctic ground squirrel as follows: ". . . from Churchill in Hudson's Bay round by Melville Peninsula, and the whole northern extremity of the continent to Behring's Straits, where specimens precisely similar were procured by Captain Beechey." Except for further extensions southward this still stands as a fairly accurate statement on distribution for the species as a whole. The race *C.p. barrowensis* represents the most northerly extension of the genus *Citellus* in continental North America. Howell (N. Amer. Fauna, 56, 1938) indicates the range for the Barrow ground squirrel as the "Arctic coast of Alaska from Point Hope eastward at least to Point Barrow; limits of range not known". Six sites of known occurrence were noted by Howell along the Alaskan Coast from Cape Thompson

to Point Barrow. Work by the present author, combined with thoroughly reliable field observations by other scientists working in the Point Barrow region, has resulted in 12 known sites of occurrence from the Kukpowruk River east to the mouth of the Anaktuvuk River, approximately 150 miles southeast of Barrow, and to the south as far as Anaktuvuk Pass in the Brooks Range (Fig. 1).The localities east of Point Barrow fill to some extent a gap noted by Howell when he stated that ". . . no specimens have been seen from points between Point Barrow and Collinson Point". It may be noted from Figure 1 that no specimens are indicated in the immediate vicinity of Point Barrow; the Inaru River, roughly 30

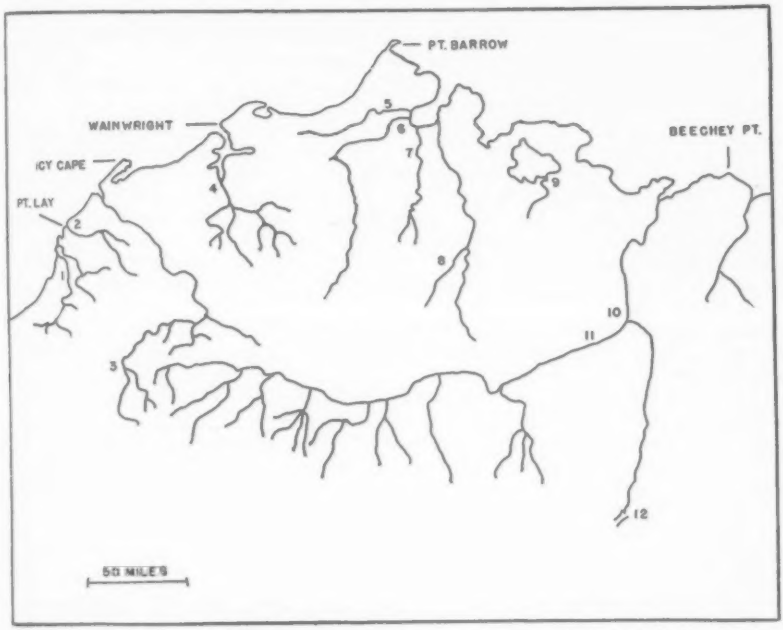

FIG. 1.—Known sites of occurrence of *Citellus parryi barrowensis* in the vicinity of Point Barrow, Alaska: 1. Mouth of the Kukpowruk River; 2. Mouth of the Kokolik River; 3. Driftwood; 4. Mouth of the Kaolak River; 5. The Inaru River; 6. The Meade River; 7. The Topagoruk River; 8. East Oumalik; 9. Mouth of the Tugley River at Teshekpuk Lake; 10. The Colville River, north of the Mouth of the Anaktuvuk River; 11. Umiat, on the Colville River; 12. Anaktuvuk Pass.

miles to the south, being the most northerly noted habitat. No squirrels have ever been noted in the immediate vicinity of Point Barrow by workers of the Arctic Research Laboratory, and inquiries of the native Eskimos reveal that none have ever been seen by them at Point Barrow, the squirrels having always been sought to the south. This information casts some doubt on the locality of those specimens in collections labeled as being from "Point Barrow", and makes it seem probable that either they were brought into Point Barrow from elsewhere for sale or trade by Eskimos or that the designation "Point Barrow" formerly took in far more territory than that to which we now limit it.

Habitat.—At first glance the flat arctic tundra appears a distinctly unfavorable habitat for a burrowing animal. The ground of the arctic slope is permanently frozen to a depth of

many feet throughout the year, except during the brief summer, when it may thaw superficially to a depth of a few inches or feet. To a genus such as *Citellus*, which in California may burrow to depths of more than five feet below the surface, the high permafrost table greatly restricts the available habitats. Even in the arctic, however, a relatively low permafrost table exists in certain areas correlated with good drainage, and within these restricted regions ground squirrels have a suitable habitat. Thus, though the coastal plain is flat, treeless, and covered with innumerable lakes, marshes, and streams, the squirrels may locate their burrows in the ridges and river sandbanks (Pl. I), hillocks, and other raised areas with a sandy soil, sandy loam soil, or sandy clay soil. Because these areas are relatively small and rather widely distributed, the coastal plain with its otherwise flat, wet soil must be regarded as a somewhat marginal habitat. Further to the south, where the land is of higher contour and affords better drainage, as at East Oumalik, favorable sites for burrows are more abundant. Squirrels have been found from almost sea level as at Teshekpuk Lake, to elevations of 2800 feet, as at Anaktuvuk Pass in the Brooks Range.

Home territory.—In respect to the home territory of individual squirrels, this squirrel is found to range over a considerably wider area than *Citellus beecheyi* of California. At Teshekpuk Lake in a period of one hour and fifteen minutes, from 11:45 A.M. to 1:00 P.M., one animal was observed traveling a distance of about 2620 yards before being lost to view. The straight line distance from the starting point to where the animal was lost to view was 1500 yards. Other animals were noted at relatively shorter distances, for example, 720 yards from their home burrows. At the Meade River site a colony of twelve animals was observed occupying an area approximately 125 by 300 yards, but utilizing a far greater area for foraging.

One of the factors that, on cursory examination, would seem to limit the range of the ground squirrels on the coastal tundra is the great abundance of bodies of water. While the burrow systems must be located in the drier ridges and sandy river banks, the squirrels can forage in the marshy centers of the tundra polygons (characteristic patterns outlined by ridges formed by ice action), and in other areas unsuitable for burrows. They not only are capable of swimming, as was demonstrated by the release of trapped animals in water, but were twice observed by the author at East Oumalik, July 31, taking to water of their own accord to cross a stream. Consequently, the presence of water cannot be considered a barrier to the distribution of the squirrels.

While no definite evidence of surface territories was noted for individual animals, the squirrels have very definite burrow preferences. Even in times of fright a squirrel will by-pass the safety of nearby burrows and undergo a longer exposure to danger to enter more familiar burrows further away. This behaviour might at first appear to be the result of following established escape paths, but one trapped squirrel, taken some distance away and released into a presumably foreign furrow, entered the burrow reluctantly, then almost immediately left the safety of this burrow, despite the presence of the author not a foot from the entrance, to run toward home territory.

Relations to humans.—As noted above, it was not uncommon for squirrels to ignore the presence of man completely when fleeing other dangers or even to ignore him while engaged in the usual activities, such as foraging. Once the animals had become accustomed to the whirring noise of the camera, it was possible to take motion pictures of normal foraging activities within eight feet.

The squirrels were easily captured with "Havahart" traps. At the Meade River, using only two No. 2 "Havahart" traps, it was possible to trap seven animals in one locality between 7:30 A.M. and 7:00 P.M. One was trapped within an hour of the setting of the traps, and the others were caught throughout the day, despite the angry chatter and warning whistle of the trapped animals. Other members of the colony watched the trapping from a short distance, or even came close to investigate the trap and the animal it contained. The catch could have been even larger, as the traps were sprung an additional ten times during this period (without effecting a capture) by wind, squirrels and faulty release action. The

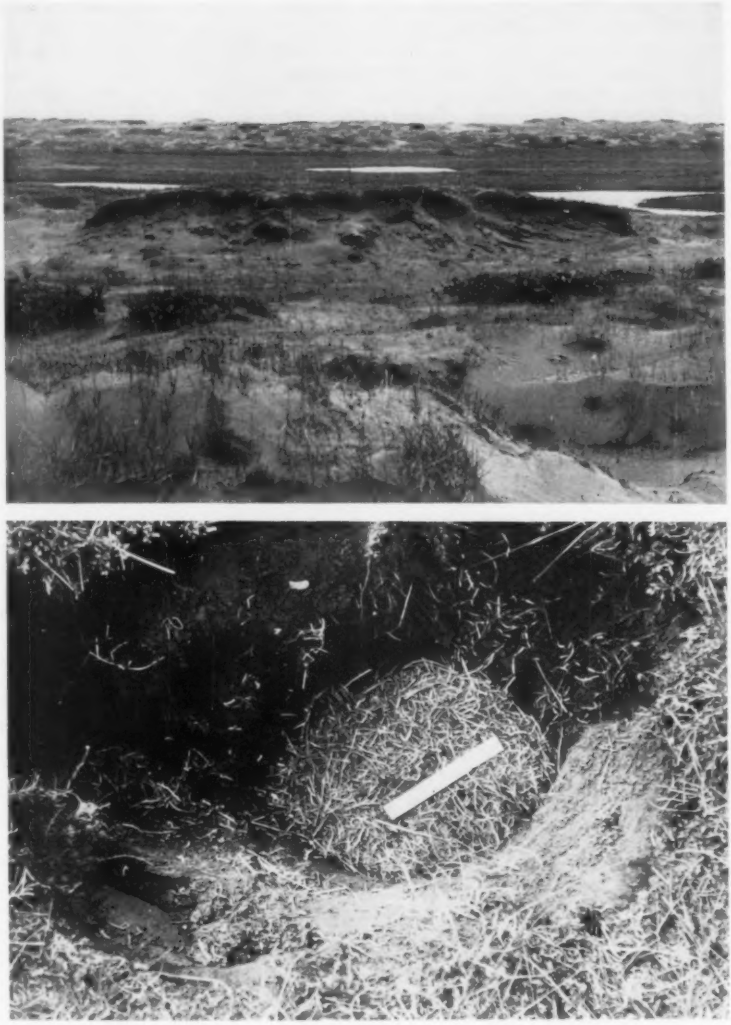

PLATE I

UPPER: Typical river sandbank habitat of *Citellus parryi barrowensis*. The elevation of the rows of dunes above the marshy tundra insures good drainage and a low permafrost table, permitting the construction of burrows. Two separate burrow systems were found on the hillock in the foreground (July 20, 1951—Meade River).

LOWER: Nest of *Citellus parryi barrowensis*. This nearly spherical nest, located on a side passage of a burrow system twenty-three inches beneath the surface, was designed for hibernation. The six-inch stick gives an indication of size (Aug. 21, 1951—Teshekpuk Lake).

squirrels' lack of fear of man and his traps, doubtless resulting from little contact with humans, was often demonstrated.

Sixteen animals were taken in the immediate vicinity of the abandoned oil camp of East Oumalik. Thirteen were prepared as skins or skeletons, two were taken alive to the zoological laboratories of the University of Southern California in Los Angeles for further study, and one toe-clipped animal was released and not recovered. These animals, like those at Meade River, were taken in a relatively restricted area. Due to the fact that the squirrels of an area share the same temporary shelters it was possible to trap several animals in one spot. Six were trapped under one portable building, and seven were seen at different times in an empty, 55-gallon-drum under the refrigerator wanigan, although only four were trapped at this spot.

The squirrels appear unwilling to leave their home area even when subjected to repeated capture and annoyance by humans, as is illustrated by the following example. An animal, caught July 31 in some discarded six inch pipe at East Oumalik, was marked on the nose and between the ears with ivory paint. On August 1 it was seen in the drum mentioned in the preceding paragraph; on August 2 it was retaken in the pipe, removed from camp, and released in a foreign burrow. August 3 it was caught again in another pile of pipes to the southwest of the camp and prepared as a study skin. It may be noted here that paint is a poor field-marking substance for these animals, for they begin removing it as soon as it is applied, and with considerable success. One animal, marked August 1, was recaptured August 2, at which time, the paint and a large patch of hair were gone.

Squirrels were frequently seen as much as a quarter of a mile away from cover of any sort. One animal, when pursued for over 300 yards, gave no indication of the existence of a burrow in the vicinity, but would run from a barrel, to a sled, to a pile of junk, to other debris or man-made structures as though thoroughly familiar with such an escape route. When chased in the opposite direction it retraced its path in reverse.

Habits.—In habits *Citellus parryi barrowensis* resembles somewhat the ground squirrels of the United States, but is sufficiently diverse in its activities to have established behavior patterns entirely its own.

The darkness of the winter days in the Arctic cannot affect the hibernating ground squirrel, but it is interesting to compare the effect of 24 hours of summer sunlight on the Barrow ground squirrel with the effect of normal light rhythms on *Citellus beecheyi*, which in California is a diurnal animal. It was observed that, despite constant light, the Barrow squirrels behaved as if in response to a regular, diurnal light rhythm. The earliest hour at which they were noted above ground was 4:10 A.M. at Meade River, July 22. The latest surface activity at Meade River was observed to occur at 9:10 P.M., July 18. Thus it is apparent that the squirrels remained beneath the surface for a period of at least seven hours. The latest hour at which any ground squirrel was noted above ground in the field was 9:35 P.M. at East Oumalik on August 1. In captivity, the squirrels follow essentially the same pattern as they do in the field, the latest time of activity at Point Barrow, when there was no undue disturbance by humans, being 9:45 P.M.

It is difficult to determine the factors that, in the absence of darkness, cause the cessation of surface activities. Variations in summer temperatures seem to have little effect on the activity of the animals, for they were active on both cold and warm days. Rain does not discourage surface activities, for they were both seen and heard frequently during rainy periods and were occasionally trapped with their pelage still wet from rain and vegetative drip.

Light intensity may be the controlling factor for, despite the fact that there are 24 hours of light, the amount varies considerably during this period, being less during the normally dark hours as the sun approaches the northern horizon. It is the belief of the author that light intensity, and perhaps a polarization of the light, may influence the evening withdrawal of the squirrels. It is planned to investigate this problem in more detail in the summer of 1952.

Although the arctic slope offers little cover, the ground squirrel tends to take advantage

of whatever amount is available. Where the vegetation is thick enough, runways can be found extending from the burrow entrances in the same fashion as for *Citellus beecheyi* in California. In other instances the cracks in the polygonal-patterned ground are utilized. However, if the squirrel were to confine its activities to those areas where an adequate protective cover is always available, the range would be extremely limited. Consequently, it is not unusual to find this animal out in the open, many yards from cover of any kind. It has been tracked across open sand dunes for as much as 100 yards and is frequently observed foraging in open country.

Correlated, perhaps, with the lack of readily available cover is a peculiar type of locomotion which was noted in walking animals. They were seen to progress by what may best be termed a crawl, walking with the body flattened dorso-ventrally, but not touching the ground. They travel in this fashion for considerable distances, looking somewhat like young badgers. This method of progression was noted at both Meade River and Teshekpuk Lake and was so frequently observed as to be entered in the field notes as the "tundra glide". When moving more rapidly this type of locomotion was abandoned in favor of a more bounding progression.

Squirrels in the open tundra often take sand baths, either in the loose sand of surface runways or before the entrance of the burrow in the loose, excavated soil. They roll in the sand like a young puppy.

Citellus parryi barrowensis has a characteristic habit of flicking its tail in a series of quick, vertical movements which are repeated at intervals of from two to 11 seconds. This behaviour somewhat resembles that observed for *Citellus leucurus* and *Citellus lateralis*. It is a habit also possessed by members of the genus *Cynomys*, with which the arctic ground squirrel has been confused by many laymen. In common with *Citellus lateralis*, the Barrow ground squirrel erects the hairs of the tail when angry so that they stand out and give it the appearance of a bottle brush.

In captivity the squirrels were inclined to bite, and were hard to handle unless special effort was made to tame them. The Eskimos at Point Barrow succeeded in making pets of those kept in captivity. When handled, the squirrels everted the anal glands in a tri-partite pattern. In captivity the animals emitted a musky odor which was discernible at some distance, although not particularly unpleasant.

The tendency to follow habitual escape paths is very evident in captive animals. At Point Barrow the squirrels were kept out-of-doors in large, screened boxes which were connected to smaller, dark, indoor nesting boxes by means of a small door which could be closed with a slide. When an animal was locked in the nesting box for examination, it ran at the closed door with full force. It then made repeated efforts to escape through the closed door, even though the entire top of the nesting box had been removed and offered an ideal, alternate escape route.

While no specific observations were made on the sensory acuity of the squirrels, their visual sense seemed poor. They ran into objects without apparently noticing them, seemed to have difficulty in locating offered food by visual inspection, and, in common with many animals, were unable to detect an observer who remained quiet. In dim light these visual difficulties seemed accentuated.

The squirrels were remarkably free of parasites. Of 23 animals examined, only one harbored a flea. Superficial, gross, visceral examination of 13 animals showed no internal parasites, nor did a thorough, gross examination of the viscera of one captive animal.

Voice.—The arctic ground squirrel is an extremely vocal animal, whose characteristic scolding chatter can be heard for many yards across the tundra. Several different vocal expressions have been noted both in the wild and among those animals kept in captivity. They do not include those expressions associated with breeding, which will be included in a future paper on reproductive behaviour.

The most common voice note heard in the field is a double-noted "keek-keek", uttered in response to a disturbance of some kind, as when the burrow is approached. This note is undoubtedly the one which has caused the Eskimos to name the squirrel the "sik-sik". The

basic double "keek" has several modifications. It is sometimes uttered with an additional note, sounding like "keek-keek-coo". Squirrels were observed to enter a tunnel, return to the entrance, utter the "keek-keek", turn back into the tunnel, utter "keek-keek-coo", and repeat this latter sound as they retreated further into the burrow system. The second modification of the basic call is a loud, scolding chatter heard frequently when the captive animal is disturbed. It begins as above, but continues into a series of shorter, lower-pitched, somewhat softer notes lasting several seconds. The best verbal representation of the expression is "keek-keek-keek-keek- etc." It seems to be associated with what could be called anger, as it is commonly heard when the animals are excessively disturbed, as when handled. It may be repeated at about two-second intervals for several minutes. It is accompanied by other manifestations of anger such as humping the back and erecting the hairs on the tail. Normally, this scolding is done with the mouth open so that the teeth and tongue are visible, but one captured animal, disturbed when feeding, was able to make the same noise with undiminished vigor while holding a carrot firmly between his incisors.

Another note, distinct from the "keek-keek", is a single, loud, sharp, piercing whistle. This was heard from captive animals when they were alarmed, but was seldom noted in the field. During one period of six days of field observations, this note was not heard until trapping operations were begun, at which time it was uttered by a trapped adult female when the trap was picked up. While it is actually a single alarm note, it is sometimes repeated as often as half-dozen times by a trapped animal.

A few other notes of warning, anger, or fear have been observed. An especially disturbed animal will utter a hiss of fear, apparently formed by exhaling air forcibly from the lungs while the mouth is held open. A slight mucus rattle accompanies this sound. Ground squirrels will also utter a growl when disturbed. Heard only once, when an animal was being handled, was still another sound, a sharp, single note best described as a bark.

Two softer sounds have also been noted. One, consisting of a series of soft "mum-mum-mum" sounds, appears to be an investigatory note and is often heard when the squirrels are approaching hand-held food. The other note, likewise associated with inquiry, is a "chir-chir-chir", which is accompanied by chattering of teeth and movement of the jaws.

Of all the sounds made by this animal the most unusual is a bird-like noise approximating a "chirp" or "chir-up". Such notes were first heard among captured squirrels at Meade River. So bird-like were the sounds that the author came out of his tent upon first hearing them with the express purpose of locating the birds making them.

While the Barrow squirrels are capable of a considerable variety of vocal expressions, they differ as do humans in their use of vocal powers. Some individuals are relatively silent, even when captured, while others keep up an almost continuous barrage of scolding, chattering, and growling. In general, the animal's location is one of the most important factors influencing this. Away from protection of burrows or cover the squirrels tend to be silent, and when chased over open ground they maintain complete silence. From the safety of cover, however, as in their burrows or other places of concealment, they are highly vocal. It was this habit of scolding from the imagined safety of cover that led to the discovery of several animals that might otherwise have gone undetected in pipes and barrels at East Oumalik.

Food.—The Barrow ground squirrels will eat almost anything. Like most rodents, however, they are primarily vegetarian. They will consume any part of a plant, devouring roots, seeds, leaves, or flowers with apparently equal relish. Previous workers have recorded foods to some extent. Howell (*loc. cit.*) summarizes these findings, noting that the squirrels eat berries of *Arctostaphylos alpina* and *Vaccinium Vitis-Idaea*, as well as seeds of *Polygonum* and *Astragalus*, mushrooms, and *Polygonum* roots. He also mentions an animal of the race *C.p. ablusus* whose stomach contents consisted of 60 per cent insect material.

At Point Barrow during the winter of 1950–51, one female adult and three young of the year were placed in outdoor hibernation cages. In June of 1951 only one young male was alive. He had apparently awakened first and, lacking food, had eaten half the mother, one other young squirrel, and the back of the head of a second young animal. This indicates that *in extremis*, they not only eat flesh, but are cannibalistic as well.

In the field they were seen to eat *Dryas integrifolia*, *Pedicularis*, *Carex*, and *Eriophorum*, to eat the leaves of *Poa* sp?, and to store the seeds of *Polygonum viviparum*. Their foraging behaviour consists of rapid exploration of the site, nervous running from place to place, stopping, and sitting up. They then grab the food plants with one or both of the forelimbs, draw them close, and bite off the tops.

Food preference studies on captured animals, which had ample supplies of prepared laboratory chow available so that starvation would not influence the choices, gave an indication of the relative palatability of certain plants. In one experiment six blocks of vegetation were placed in a cage at 8:00 P.M. By 8:00 A.M. the following day the block of *Petasites frigidus* had been completely consumed, *Dupontia* and *Arctophila* were partially consumed, while *Arctagrostis*, *Poa* and *Salix polaris* (*rotundifolium*) were only 50 per cent consumed eight days later. The squirrels will take almost any offered greens, e.g., *Hierochloe*, *Alopecurus* and three saxifrages, *S. cernua*, *S. foliolosa*, and *S. punctata* subsp. *nelsoniana*. They will also take such items as lettuce, celery, cabbage, carrots, apples, oatmeal, poppy seeds, and other fruits, roots, and seeds, as well as camp supplies, such as bread and butter.

In foraging, the squirrels may fill their cheek pouches to the limit, and then gather a mouthful of dry grass to utilize in nest building upon returning to the burrow. One animal, feeding from ground baited with poppy seeds, was examined and was found to have filled the cheek pouches until they measured 6 cm. in length and 3½ cm. in width. The weight of the contained poppy seeds in both pouches was three-quarters of an ounce.

Water is so abundant on the tundra, and the burrow systems are almost always located in such proximity to it that securing adequate water constitutes no problem. Animals kept in captivity drink very freely and, if deprived of a water source for a day or so, they eagerly and thirstily accept any water offered.

Burrow systems.—The types of burrows occupied by *Citellus parryi barrowensis* are similar to those described for the California ground squirrel by Grinnell and Dixon (Bul. State Comm. Hort., 7: 597–708, 1918) and later by Linsdale (The California Ground Squirrel, 1946). In favorable habitats, such as the sides of banks or the surface of well drained, flat ground, burrow openings are numerous. Fifty-six openings were observed in one area approximately 50 yards square.

The largest of the colonial burrows excavated, consisting of 68 feet of tunnel on three levels, was contained within a rectangle 13 by 14 feet. It possessed 6 openings and reached a maximum depth of 3 feet 2 inches below the surface. A colonial burrow at another site, with a maximum depth of 2 feet 6 inches, consisted of 32 feet of tunnel within a 10 by 15 foot rectangle. This system had only three openings. A nesting burrow, in a plot 21 by 9 feet (Fig. 2), contained 3 openings (one of which was plugged), 2 nests, and 38 feet 8 inches of tunnel, which reached a depth of 2 feet 5 inches. The greatest depth beneath the surface of any burrow system observed was 3 feet 8 inches, attained in the soft sand of a dune. As noted in the introduction, the burrows were not as deep as similar ones noted for the California ground squirrel, excepting those dug into the sides of sand banks at a considerable distance below their crests.

Short, shallow, simple burrows similar to the "bachelor burrows" described by Grinnell and Dixon for *Citellus beecheyi* occurred on the periphery of population concentrations. These burrows had only one entrance and no nest, and consisted of a single tunnel, which might extend for a length of 10 feet and a depth of 2 feet 7 inches.

The burrows were very clean, feces and urine being deposited in special side passages. The burrow openings varied in size but were almost always wider than they were high. Newer systems had smaller openings, which were gradually expanded, funnel-wise, as the squirrels literally knocked the corners off by use. The largest of the older openings were over 8 inches wide and about 6 inches high. The smallest opening through which a squirrel in the field was seen to pass was a circular hole 2¼ inches in diameter in a discarded 55 gallon oil drum. The smallest burrow opening observed in the field was 4 inches wide by 2 inches high.

One burrow had a shallow form scooped out in front of it in the excavated dirt. This form, 20 inches from the opening of the burrow, measured 9 inches long by 4 inches wide and 4

inches deep. It was used as an observation post, and its occupant crouched down in it in much the same manner as a hare.

The speed at which a ground squirrel is able to dig its burrow obviously varies with the type of ground through which it must travel. In soft sand at the Meade River site, an animal was observed to dig 37½ feet in a period of less than 24 hours. In burrowing through soft sand, the squirrel takes advantage of the roots of *Salix*, which greatly strengthen the roofs of tunnels dug beneath them, and complicate the problem of exposing the burrows from above.

Nest.—The chief material used in the construction of the nest is dry grass, but lichens, ground squirrel fur, caribou fur picked up on the tundra, and a few green leaves have also been found. The nest almost completely fills the nesting chamber, a room which may vary from proportions of 14 inches wide and 6 inches high, to an almost spherical shape of 10 by 11 inches. The nesting chamber may be on a side passage from the main one and have two entrances (Plate I), or it may mark the termination of the passage and have only one entrance. The nests observed were all clean, with no scats or urine smell in evidence. There was no indication of drainage tunnels extending beneath the nests to carry off excess mois-

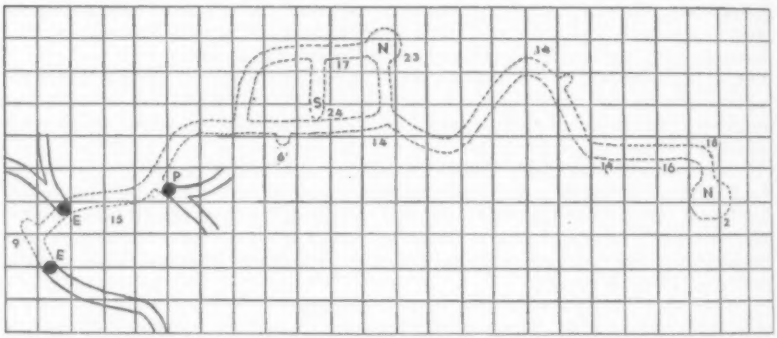

FIG. 2.—Nesting burrow of *Citellus parryi barrowensis*. Each square equals one square foot. Dotted lines outline the underground burrow. Solid lines indicate the surface runways. E, Entrance; P, Plugged entrance; N, Nest; S, Site of scat deposition. Numbers indicate the depth beneath the surface, in inches.

ture, but it is to be remembered that the burrow sites are always located in areas of good drainage. In addition, much of the precipitation occurs as snow, the precipitation total for the year measuring only about six inches and not necessitating an elaborate drainage system. Two nests were found at the Teshekpuk Lake site in August which were only 2 feet, 5 inches, and 1 foot, 11 inches below the surface yet were obviously designed for hibernation. The squirrel had been observed carrying in mouthfuls of dry grass for the construction of the nests and storing seeds of *Polygonum viviparum*, which were later removed from both nests in large handfuls.

Young.—The only known litter born in captivity was one composed of two females and four males born at Point Barrow, in June, 1950, after a gestation period of about 25 days. In June of 1951, four pairs of squirrels at Point Barrow were placed in separate cages for a week, but no issue resulted from this pairing. Recent observations on captive animals at the University of Southern California lead the author to believe, that, very probably, the period of heat is restricted to a relatively short time early in the year. This may be to insure that the young develop sufficiently during the first summer to successfully enter hibernation in the fall. Some measure of litter size is given by the number of placental scars found in two females trapped June 14 and 15 near the mouth of the Anaktuvuk River, those in one animal numbering 6 (4 R; 2 L), those in the other, 7 (5 R.; 2 L.).

An indication of the distribution of the age and sex groups within a restricted area is obtained by consideration of 15 squirrels captured at the Meade River site. Of 8 animals trapped here July 22 and 23, 3 were adults and 5 were young, 6 were female and 2 male. In addition to the trapped animals, four other young were noted in this area, approximately 125 by 300 yards, making a total population of at least 12 young and 3 adults. The young observed in the field were playful as kittens, and would chase one another, roll, mock-fight, and engage in thoroughly active play. They also displayed adult mannerisms such as sitting up with the forelimbs directed downward over the chest while observing the surrounding terrain.

At East Oumalik, 9 females and 6 males were captured between August 2 and 7. By Meade River standards of weight none of these was a young animal, the lightest animal weighing 552.6 gm., whereas the heaviest young of the year at the Meade River weighed 283.4 gm. As it is very unlikely that none of the 15 East Oumalik animals were young of the year, we may tentatively conclude that the distance of 60 miles to the south, together with two weeks additional time, was sufficient to advance growth far beyond that at Meade River. If this conclusion is correct, the squirrels to the south doubtless survive better through the winter, due to their greater development, and the more northerly areas must represent a somewhat marginal habitat.

In the vicinity of Point Barrow, the most favorable calculations for the growing time alloted to the young of the year is four months, assuming early emergence of adults by May 1, immediate mating, and birth of the young in June. This also assumes that hibernation will not begin until October, which is a fairly late date. The time of hibernation varies in different parts of the range, and is also dependent to some extent upon the degree of severity of the winter. Squirrels have been reported above ground in the Arctic as late as December 3 (Howell, *loc cit.*). According to the Eskimos, the squirrels go into hibernation in September and do not emerge until April. In captivity in Los Angeles, their body temperature dropped from a figure of 36.4°C. to 17.0°C. During hibernation in captivity each squirrel rolls into a ball, with the dorsum uppermost. The squirrels are actually sitting on their haunches with the tail curled under the body and forward up over the head. Their respiration is not perceptible, and they can be handled without awakening them. Evidence that hibernation is not a foolproof way to escape the rigors of an Arctic winter is the fact that two animals froze to death in the animal quarters at Barrow during the winter. This suggests a certain mortality among animals in the field who have failed to provide properly against the rigors of the Arctic climate, especially among the young of the year, who do not have a second chance to rectify the errors of their first wintering burrows. A later report will treat hibernation in more detail.

Growth.—Five young of the year trapped at Meade River, July 22 and 23, averaged 272 gm. in weight, the four females averaging 272.6 gm. and the one male weighing 269.3 gm. In captivity the squirrels tend to acquire an excess of fat, making comparison with field-trapped animals difficult. However, weights taken for captive animals of three known age groups give some indication of growth. Three animals thirteen months old averaged 850 gm., the two females averaging 864 gm., and the one male weighing 821.8 gm. The weight of six animals kept in captivity for a year averaged 940.9 gm., the three males averaging 1028.7 gm., while the three females averaged 850 gm. Three animals kept in captivity for two years averaged 873.7 gm.; two males averaged 921 gm. and a female weighed 779.3 gm. Thus by the end of one year the young have virtually reached their total adult weight and will gain little more during their second year. In the first four months of their life they gain enough weight to enter hibernation in the fall. Captive young which averaged 272 gm. when trapped in July, averaged 877 gm. in Los Angeles in October, showing a gain in weight of 222.4 per cent in less than three months. By the second summer they are indistinguishable from adults in weight. Weights of animals trapped at the Meade River showed that the young increased from 283.4 gm. to 694.3 gm. from July of one year to July of the next. The largest young of the year at this site had attained a length of 320 mm., while the smallest adult measured 348 mm.

Forty-seven captured ground squirrels presented a ratio of 20 males to 27 females, or

74 males:100 females. Average measurements of twenty-nine adult squirrels in millimeters were 393.2 (348–435); 114.4 (88–135); 62.7 (55–68); 14.8 (10–19). (The ear measurement was based on only 27 animals.) The average measurements of sixteen female adults were 385.3 (348–425); 111.3 (88–135); 61.1 (55–64); 15.1 (12–19). The measurements of thirteen male adults were 403 (377–435); 118.2 (105–126); 64.7 (60–68); 14.3 (10–17). (The ear measurements in each case were based on one less animal.) Average measurements of six young of the year in July (five females and one male) were 313 (304–320); 95.2 (85–101); 56.8 (55–59); 9.8 (8–14). Average measurements of the male adults exceeded those of the females by 4.6 per cent in length, 6.2 per cent in tail length, and 5.9 per cent in hind foot. The females exceeded the males in ear length by 5.6 per cent. The weights of eleven field-trapped female adults averaged 698.5 gm., and those of eight field trapped males averaged 790.7 gm., the average weight of the males exceeding that of the females by 13.2 per cent. The greatest maximum weight of a field-trapped animal was 906.9 gm. as contrasted to a maximum of 1133.6 gm. for captive animals.

The squirrels are used by the Eskimos for both food and clothing. The amount of meat which may be obtained from them is indicated to some extent by statistics gathered at East Oumalik. On seven animals captured in August, subcutaneous fat made up 6.09 per cent of the body weight, averaging 49.6 gm. of a total body weight average of 813.3 gm. Nine animals whose average weight was 761.8 gm. were dressed out. Their average dressed weight was 340 gm., indicating that 44.6 per cent of the body weight is retained in a dressed carcass.

SUMMARY

The data for this preliminary life history study of the Barrow ground squirrel, *Citellus parryi barrowensis*, were gathered at Point Barrow, Alaska, within Naval Petroleum Reserve No. 4, from July 12, 1951, to August 28, 1951.

Twelve positive sites of the squirrels' occurrence, located from almost sea level to an altitude of 2800 feet are recorded. Their range of distribution is definitely extended 150 miles east of the limits set by Howell (*loc. cit.*). Within this range the squirrels' habitat requirements of a relatively low permafrost table and good drainage restrict their burrow systems to river banks, hillocks and similar areas raised above the coastal plain. The presence of numerous bodies of water on the tundra does not confine the animals to the vicinity of the burrows, for they not only are capable of swimming but will take to water of their own free will. They have been observed to travel over 1500 yards from their home burrows. No surface territoriality was observed among the squirrels, but they have pronounced burrow preferences.

They show little fear when they encounter man, are easily trapped, and, due to their common sharing of temporary cover, several may be taken at one spot.

Despite twenty-four hours of sunlight during the summer months, the squirrels behave as if in response to a diurnal light rhythm. The latest surface activity noted in the field was at 9:45 P.M. and the earliest was at 4:10 A.M., the intervening hours being spent beneath the surface.

The squirrels take advantage of whatever cover is available on the tundra, but as sufficient cover does not exist for such widely ranging animals, it is not unusual to find them in the open, far from any available shelter. A peculiar type of crawling locomotion which they have been observed to use may be the result of trying to appear inconspicuous on the open tundra.

The squirrels are highly vocal, and have at least ten different sounds in their

repertoire, not including those of the breeding season. These sounds vary from a harsh scolding to a bird-like chirping.

The squirrels feed on berries, seeds, roots, and leaves of at least 16 native plants, and, in captivity, they adapt themselves well to a laboratory diet. A generous supply of water is a necessity in captivity.

The burrows of the Barrow squirrels are similar to those of the California ground squirrel except that they are shallower, being limited in depth by the permafrost table. The greatest depth of any burrow investigated was three feet, eight inches below the surface, and nests built for hibernation were found to occur at depths of less than three feet. The burrow systems had side passages for the deposition of feces and urine, and the nests were clean and free of unpleasant odors.

The young are born in June and grow rapidly, developing sufficiently to enter hibernation in October at the latest. By the end of summer they have reached adult size, gains after the first year being slight.

The sex ratio was 74 males : 100 females. Males were larger and heavier. Animals kept in captivity for a time were found to exceed by 200 grams, or more, the weight of squirrels of similar age caught in the field. When dressed, the squirrels retained 44.6 per cent of the total live weight.

Department of Zoology, University of Southern California, Los Angeles. Received May 6, 1952.

A POPULATION OF THE JAPANESE FIELD VOLE INFESTED WITH TSUTSUGAMUSHI DISEASE

By Ryo Tanaka and Seiyu Teramura

The Japanese field vole, *Microtus montebelli* (Milne-Edwards), is a prolific, wild rodent prevailingly inhabiting the lowlands of Honshu, but it has as yet been found relatively uncommon in Kyushu and absent in Shikoku. The vole is a serious agricultural pest, and is associated with the occurrence of tsutsugamushi disease (scrub typhus) in central and northern Honshu. Some observational data on the breeding and feeding habits, burrow systems, and predators of the vole in the endemic and non-endemic areas were previously reported (Kawamura and Ikeda, 1935; Watanabe, 1937). The fact that biological research on the trombiculid mites, vectors of the disease, has markedly progressed since the last war necessitates the elucidation of the epidemiological role of the vole from more precise knowledge of its population ecology. Roonwall (1949) lately studied the relative abundance in various habitats of the mite-bearing mammals in Assam.

We marked and released individual voles to estimate the home range and population on a brushy riverside on the upper reaches of the Omono River, about four kilometers south of Omagari-Machi, Akita-Ken, in the north of Honshu, long known as one of the notable endemic districts infested with the typhus.

This was done through a fortnight in the mid-summer of 1951, which is the most important season from the standpoint of epidemiology.

Many thanks are due Dr. M. Sasa, Institute for Infectious Disease, Tokyo University, for his helpful suggestions and partial financial support.

Study area and trapping record.—A quadrat of about two acres was laid out on a grassy area mixed with tiny shrubs, in which the vegetation was mainly formed by *Miscanthus japonicus*, *Artemisia* sp., *Salix gracilistyla*, etc. The plot was surrounded by identical conditions except for the western side bordering on a cultivated field, allowing movement in and out by voles on every side. The area was occasionally flooded. Forty live-traps used were made of wire net, other methods employed being the same as before (Tanaka, 1951; 1952). Traps of this type proved no less efficient for the voles than box-traps. The vole was the exclusive rodent in the area.

The trapping record obtained is shown in Table 1. As denoted in the table, almost every day one to three specimens were caught dead in the trap or died before released. Death was due partly to the attack of predators, perhaps *Mustela* sp., which were certainly inhabiting the tract, and partly to careless exposure of the vole to sunshine. It is possible that the carcasses without wounds occurring occasionally in the traps under grassy cover have some relation to the latent epizootic, because most of the field mice in the endemic area have been confirmed to be a reservoir of the pathogene (Kawamura and Ikeda, 1935). But no apparently ailing animal was met with in the study field. Needless to say, nearly all captures were more or less heavily parasitized by the efficient vectors, the larval mites or *Trombicula akamushi*, at least on the ears.

As in other mice and rats (Burt, 1940; Davis and Hall, 1951), the breeding activity of this vole indicated a peak in spring and autumn and a slump in winter and summer. In practice, mid-summer captures of some individuals with the size and coat color of distinct adult type were made with scrotal and vaginal conditions suggestive of non-breeding activity, so that immature animals or juveniles were often difficult to distinguish from young adults in the field. A specimen with adult color and more than half grown, but not fully adult in size, was reckoned as a young adult, unless any other status was distinct.

Of the captures, 35 were males and 32 females; the slight excess of males reflects the trend, referable to a greater wandering tendency of the males (Tanaka, 1951a), seen in the meadow vole and other mice and rats (Burt, 1940; Davis, 1951; Davis and Hall, 1951). There was, of course, no significant departure from the 50 per cent ratio of males. A reverse sex ratio, smaller than 50 per cent males, however, has previously been presented for this vole by Watanabe (1937). The sex ratio has never differed significantly ($P > 0.1$) from 50 per cent males in this vole except for the adult captures by Watanabe, in which the females outnumbered the males significantly ($0.05 > P > 0.02$). The latter ratio, which is inconsistent with our common knowledge, might have been brought about by his misjudgment of young adult animals for the reasons noted above.

Home range.—From the small study area and the lower trapping record in the beginning of the work (Table 1), the data available were not sufficient for the

estimation of a complete home range. Of 39 recaptures (58 per cent of captures), 19, 11, 6, and 3 were caught two, three, four, and five to eight times respectively. The home range was computed by the boundary strip method as before (Tanaka, 1951; 1952); the size thus determined will rise to a certain limit by increasing the number of times of capture and the distance between traps, according to Hayne (1950). We obtained as a mean area in acres 0.14 (0.06–0.28) from 15 adult voles captured three or more times, 0.16 from three adults taken five or more times, and 0.08 from three juveniles taken four times. Therefore the adult average of 0.14 acre will probably be not much less than the full value that may be gained with a trap interval of 15 meters as in the present work. It is grossly equal to 0.15 acre for *Clethrionomys* near the top of Mt. Ishizuchi (Tanaka, 1951), but is half as small as the 0.2–0.5 acres estimated by Blair (1940) with

TABLE 1.—*Trapping record for Microtus montebelli in the endemic area in Akita-Ken*

DATE (1951)	CAPTURES			TOTAL NUMBER PREVIOUSLY MARKED (x)	RATIOOF CATCH PREVIOUSLY MARKED (y)
	New	Previously marked	Total		
July 30	3**	0	3	0	0
" 31	3	1	4	1	0.25
August 1	9**	1	10	4	0.10
" 2	5(1)*	4	9	11	0.44
" 3	8(3)	6*	14	15	0.43
" 4	12(4)	8*	20	22	0.40
" 5	9(1)*	9*	18	33	0.50
" 6	10(1)*	12***	22	40	0.55
" 8	2(2)	16*	18	46	0.89
" 9	3	11**	14	47	0.79
" 10	3	8**	11	48	0.73
Totals	67(12)		143		

* One, ** two and *** three animals dead in the respective group of captures. The figure in the bracket shows the number of juveniles included in the new captures.

nearly the same trap interval in the meadow vole in Michigan. The calculation of our values for *Microtus* and *Clethrionomys* was, however, based on a small trapping area, whereas the area trapped by Blair was fairly large (totaling 20.4 acres), hence our values may have been under-estimated because only parts of the home ranges of animals living near the border of the plots were taken into the calculation. The effects of these would be minimized by working in a larger area. For the meadow vole, Hayne (1950) estimated 0.12–0.16 acres with a trap interval of 40 feet in 2.4 acres under traps, but 0.21–0.58 acres with a trap interval of 60 feet in an area of 4.6–8.1 acres. A small range of 0.07 acre was given by Hamilton working in small areas approximating an acre. Consequently the ultimate size of home range for the Japanese field vole will presumably be larger than 0.14 acre and close to that of the meadow vole, and also a like inference would be possible for Smith's vole. Although a sexual difference in mean

size of home range was not found, a greater cruising tendency for the males than for the females and juveniles can be seen in the frequency table (Table 2) of moving distances measured from the site of the penultimate capture. Moving 96 meters by an adult male was regarded as wandering beyond its home range.

TABLE 2.—*Moving distance of voles recaptured two or more times*

DISTANCE IN METERS	RECAPTURED AT:	ADULT MALE	ADULT FEMALE	JUVENILE
0	The same site	13	24	16
15	The adjacent site	9	3	1
21.5		3	0	0
30	The distance of two trap intervals	0	1	0
33.5		0	1	0
45	The distance of three trap intervals	0	1	0
48		2	1	0
96	Beyond home range	1	0	0
Average distance moved:		14.0	6.5	0.9

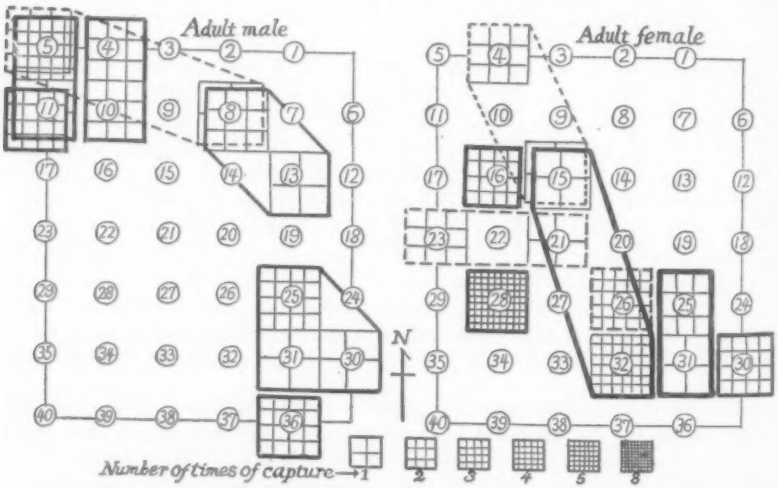

FIG. 1.—Outlines of home ranges of adult voles, taken three or more times, drawn by the boundary strip method; the cross-hatched square formed by the lines half-way the trap interval shows the number of times of capture for each vole at the trap site (circles with trap numbers).

The complete home range of each vole will tend to more broadly overlie those of other members, since the apparent home range, possibly underestimated, is seen from Figure 1 to indicate overlap among many adult voles. Nevertheless, if we inquire into the distribution of the most densely shaded square within each home range, allowing for the assumption (Blair, 1942), in conjunction with

the idea of center of activity (Hayne, 1949), that the trap in which a vole is taken most frequently is nearer to its home site than are others, the square can be found to be in most cases isolated from others. Thus we can interpret that the territory, in view of Burt's (1943) conception, is restricted to the neighborhood of the nest site, and is established among females as well as among males, and to a lesser degree even between both sexes. One case of overlap occurred in males after the death of the preoccupant. The home site of the young also seems to be isolated from those of adults. In consequence, we suspect that this vole has, as a whole, a trait of intolerance between members of the population, and that a pairing of breeding adult voles is of short duration; in fact, no instance of a simultaneous catch of two adults in the same trap was encountered.

Population estimate.—As in our previous papers (Tanaka, 1951; 1952), the population was estimated by the parabolic formula applied to the values for x and y in Table 1, and P = 120 and β = 0.42 were computed. The census was based on all captures of all sex and age classes, and mixed with some non-residents, because it would seem inaccurate to distinguish residents from immigrants or transients because of the few number of times of capture. The estimated value of P is almost twice as large as the total of new captures (Table 1), and the amount of the mark-and-release index reveals that the behavior pattern in this vole toward traps is more intensely of Type I (Tanaka, 1951; 1951a, 1952) than it is in *Clethrionomys* (β, 0.61–0.72), i.e., the degree of probability for marked voles to enter the trap over that for unmarked is greater in the former species. The trend is expressed by the notable departure of the theoretical curve from the hypothetical line in the figure. The behavioristic traits of this vole suggest that, because they are so difficult to mark completely during a short trapping period, the census by totaling new captures may be exceedingly under-estimated.

For calculating population density, when we used a home range of 0.14 acre with a marginal strip of 12 meters around the plot, a population of 43 per acre was estimated, and when 0.35 acre (average of 0.2–0.5 acres) with a marginal strip of 18 meters was used as an area approximating a complete home range, 34 per acre were estimated. Therefore, the population has proved notably denser than that of *Clethrionomys* on Mt. Ishizuchi, and the density is also much greater than the maximum size (14.6) for the meadow vole reported by Blair (1940). It is not to be strictly compared with the latter on account of a difference in the census method. However, if our value of the total of new adult captures divided by the area under traps is compared with Hayne's (1950), our value is within the range (12–90) of the latter's. Furthermore, Hamilton (1937) estimated a vole population in the spring of 1933 in Ithaca as 15–40 per acre dependent on habitat. Accordingly we might well think that an ordinary population of the meadow vole in northeastern America may be close to the above value presented by us.

Epidemiological significance.—The home range of the vole could not be conclusively estimated, nor could the population density be definitely revealed. The home range average is between 0.14 and 0.35 acre and a complete range is presumed to be rather nearer 0.35 acre, which is a mean size for the meadow vole.

Therefore the population per acre is estimated to be as high as 34 to 43. Thus we have found that this vole is likely to be more or less comparable with the meadow vole in northeastern America in behavior pattern toward traps, home range, and population. Nevertheless, the home range and population figures obtained by us were those for mid-summer, and little is known of their seasonal shift. Blair (1940) reported that a maximum population of the meadow vole was reached in July of a period from late May to September in his tract, hence the

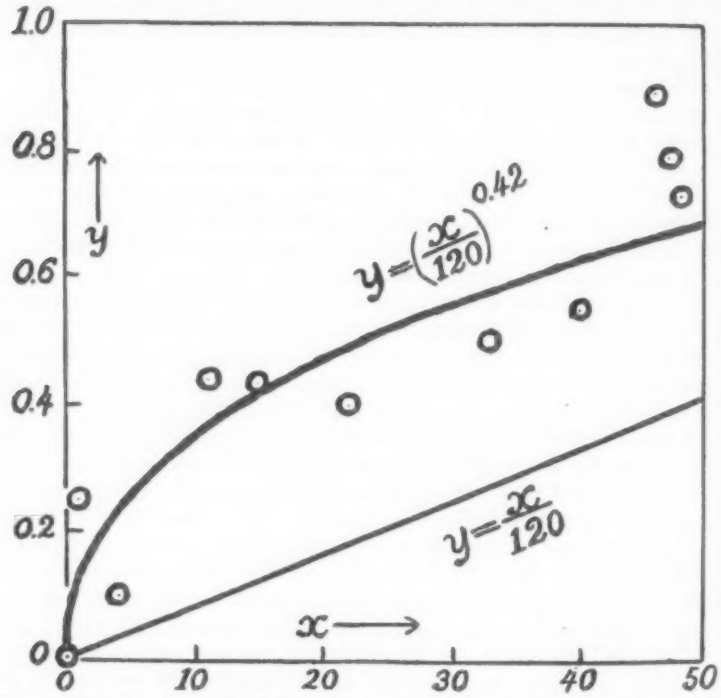

FIG. 2.—Plot of x on y, and the theoretical curve followed by the hypothetical straight line.

mid-summer population of our vole would supposedly be also near the peak for the year.

The numbers of this vole on the brushy riversides in Akita are obviously greater than that for any other vole or mouse that has hitherto been studied in Japan, and it seems probable that a crowded population of this vole likewise inhabits the endemic areas. These areas are occasionally flooded, and are covered with similar soil and vegetation in other localities in northern Honshu. We must attach the most importance to the mid-summer populations from the view-point of the epidemiological role of the vole, because it is recognized (Sasa, 1951:

Teramura, 1952) that cases of tsutsugamushi disease occur with the highest frequency in accordance with the greatest occurrence of *Trombicula akamushi* in this season of the year. Roonwall (1949) explained that the normal mammalian hosts of the mite must play an important role in the spread of the disease in two ways: by acting as additional reservoirs of the pathogene; and by acting as vehicles for the spread of the vectors. He claimed that the relative abundance of such mammals offers to some extent a "risk index" of infection. Therefore it seems clear that concentrated populations of the Japanese field vole make an important contribution to the occurrence of abundant mites and pathogenes, giving rise to the yearly outbreaks of the disease among humans.

The annual incidence of the disease in humans appears to be sporadic and changeable within the endemic locality; this phenomena might be partially elucidated from the migration and dispersal from its home range of the vole harboring pathogenes. According to Burt (1943), territorial behavior is important in limiting the population in an area, and bringing about the dispersal of animals over a geographic area. Some indication of a restricted territory around the nest site, in which the burrow system was known (Kawamura and Ikeda, 1935) to cover about six square meters, was discovered in this vole, but we are as yet ignorant of how long the same home range or territory is kept by any vole and in what manner members may migrate from place to place.

Summary.—A population of *Microtus montebelli* was studied in an endemic area infested with tsutsugamushi disease in northern Honshu, Japan, in the midsummer of 1951.

The vole proved likely to be more or less comparable with the meadow vole in northeastern America in several ecological features. The mark-and-release index was 0.42, intensely indicative of Type I in the behavior pattern toward traps, and the home range was computed as 0.14 acre. A complete range was supposed to be rather nearer 0.35 acre in average, therefore the population per acre was as high as 34 to 43.

Some evidence for a restricted territory near the nest site was exhibited.

The epidemiological role of the vole is discussed.

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ANALYSIS OF HOME RANGE FROM RECAPTURE DATA

BY DAVID E. DAVIS

The extent of home range of a variety of animals has been studied, but few generalities have resulted because of the difficulty of comparing data that were taken by different methods, recorded in different ways, and obtained in different habitats. This paper discusses some of the difficulties involved and makes some suggestions for collection of data.

Home range data are generally obtained by recapturing marked individuals, although data may sometimes be accumulated from feces or other methods. The animals are captured, marked individually, and liberated at the location of original capture. The traps may be set in a grid or randomly. The grid system has been popular and has been critically reviewed by Mohr (1947) and Hayne (1949, 1950). Hayne points out that an animal's home range does not necessarily coincide with the distribution of traps, the home range may extend beyond the grid or the traps in which the animal was caught, and that the home range cannot be calculated for animals caught in traps that are in a straight line. Additional disadvantages of the grid system are the great labor of laying out the grid itself, the necessity of setting some traps in obviously unfavorable locations, and the need to recapture a single individual many (about 15–20) times

to obtain adequate data. Mohr (1947) has already pointed out that few animals utilize all their home range but most follow more or less definite pathways. Howard (1949) objects to the grid method because the extent of the range may not be shown. Another type of disadvantage in the results of grid trapping is that little idea of the intensity of use of the various parts of the home range is gained.

Another popular method of recording movement data is in terms of frequency of maximum distance between captures (Evans and Holdenreid, 1943). This method does not indicate relative frequencies of short travels and may merely indicate the dispersal movements within the area trapped.

A method that is not handicapped by some of these difficulties is the utilization of distances between captures. The traps are set in likely places, randomly in terms of distances, and the distance between the recaptures is recorded. The data may be analysed according to distance of recapture from the original capture or distance between successive captures (Davis, Emlen, and Stokes, 1948). The latter method is preferred because it prevents an aberrant location of original capture from biasing the results, and also minimizes the distortion due to changes in home range. However, at least for some species (Young, Strecker, and Emlen, 1950), both methods give essentially the same results. An important aspect is that it is not necessary to capture the same individual many times. This advantage is essential for species with high death rates or dispersal rates, or for species that avoid recapture. The method has some disadvantages common to all methods. Movements within the home range cannot be distinguished from dispersal movements and the animal does not travel in a straight line between captures. It is important to note that the method does not give the home range of a particular individual but an average index for the species and location. It is primarily useful for comparative purposes.

Analysis of the data consists merely in setting up a frequency distribution of the distances between successive captures. Data of this type are presented in Table 1 for Norway rats (*Rattus norvegicus*) captured on a farm near Baltimore from September, 1949 to November, 1951. The farm consists of four buildings containing race horses and cows. The rats were captured in box traps, marked by clipping toes, and released at the spot of capture. The traps were set for three to four days on alternate weeks. This is the same farm discussed by Davis *et al.* (1948). Table 2 summarizes the data in terms of certain distances.

It will be noted at once from Table 2 that the females tended to move shorter distances than did the males, and further that, in general, the extent of movement increased with age. The extensive movements (more than 126 feet) are probably dispersal rather than home range. While these conclusions seem satisfactory at first glance, a more critical examination reveals several difficulties. From a statistical viewpoint the data are unsatisfactory because they are not normally distributed. Even the transformation of the frequencies to logarithm of frequency does not give a normal distribution.

From the biological viewpoint there are a number of difficulties: (1) animals don't travel in straight lines between captures; (2) animals may learn to go into

traps for food, and hence give too many short distances; (3) traps may not be suitably spaced to indicate maximum movements; (4) transients are included; and (5) the data give only an index of home range.

In an attempt to understand this type of data a simple model was developed. "Traps" were placed at random on a sheet of paper and circular "home ranges" of two sizes were drawn on a transparent sheet for overlaying. The "home range"

TABLE 1.—*Distances of successive recaptures of rats*

MIDPOINT DISTANCE IN FEET	PERCENTAGE OF TOTAL RECAPTURES					
	Adult		Subadult		Immatures	
	Male	Female	Male	Female	Male	Female
6	34.5	44.4	42.1	46.7	44.7	50.0
18	7.3	5.3	2.4	6.1	5.1	11.0
30	22.6	23.2	24.2	24.6	18.5	11.0
42	11.4	14.4	9.0	7.3	13.9	9.3
54	8.5	5.6	5.7	3.4	7.0	4.6
66	4.3	5.3	3.2	4.4	3.6	4.6
78	2.1	0.8	1.9	2.7	1.5	4.6
90	2.1	0.6	2.8	0.7	1.5	1.9
102	0.9	0.7	1.9	1.0	0.5	1.9
114	1.3	0.4	0	1.0	0	1.9
126	0.8	0.4	1.4	0	1.0	0.9
138	1.8	0.4	1.0	0.5	1.5	0.9
150	0.1	0.1	0.5	0.3	0	0
162	0.1	0.1	0	0	0.5	0
174	0.8	0.1	0.5	0.5	0	0
186	0.1	0.1	0.5	0.3	0.5	0
198	0	0.1	0	0.3	0	0.9
210	0.1	0.1	1.4	0.3	0.5	0
222	0.1	0	0.5	0.3	0	0
234	0.1	0	0	0	0.5	0
246	0.1	0	0	0	0	0
258	0.1	0	0	0	0	0
270	0	0	0.5	0	0	0.9
282	0	0	0	0	0	0
294	0.1	0	0	0	0	0
306	0	0	0	0	0.5	0
318	0	0	0	0.3	0	0
Total recaptures	975	893	211	411	194	108

overlay was placed on the "trap" sheet in a random manner a number of times, and the distances between traps within each "home range" circle were measured. The data are given in Table 3 for "home ranges" of 100 feet and of 150 feet. It is at once apparent that the frequency of distances increase at first in both cases. This increase is not reasonable and does not agree with the data for rats or other species. The solution to the problem lies in a consideration of the number of opportunities for capture at each distance. The frequency distribution of

distances between traps is approximately a normal curve and shows that there were few chances to recapture the animal at short distances. Hence it is desirable to divide the number of recaptures at particular distances by the number of chances of recapture at these distances. When thus corrected the figures decline in a reasonable way (Table 3).

Another aspect is that rarely do the recapture distances approach the known limits of the home range (100 ft. or 150 ft.) even though there are plenty of traps at these distances (Table 3). Examination of the overlay on the trap sheet

TABLE 2.—*Percentage of recaptures of rats at specified distances*

	NUMBER OF RECAPTURES		PERCENTAGE AT LESS THAN 12 FT.		PERCENTAGE AT MORE THAN 126 FT.	
	Male	Female	Male	Female	Male	Female
Immature	194	108	49.8	61.0	4.7	2.5
Submature	211	411	44.3	52.8	6.3	2.4
Mature	975	893	41.8	49.8	4.4	1.4
Totals	1380	1412				

TABLE 3.—*Synthetic recaptures*

MIDPOINT OF RECAPTURE DISTANCE	FREQUENCY OF DISTANCES "Home Range" size		CHANCES	RECAPTURE PER CHANCE	
	100 ft.	150 ft.		100 ft.	150 ft.
10	22	28	4	5.5	7.0
30	31	54	9	3.5	6.0
50	46	87	22	2.1	4.0
70	22	43	10	2.2	4.3
90	8	36	11	0.7	3.3
110	1	37	22	—	1.7
130	—	21	22	—	1.0
150	—	4	35	—	0.1
170	—	0	29	—	—

shows that rarely does the home range include traps at the extremities of the home range and hence such recaptures are rarely possible.

This synthetic model suggests that recapture data of this type should be analyzed according to the number of chances of recapture at various distances. To obtain the number of chances it is necessary to locate each trap and measure its distance from other traps. Distances greater than the home range of the animal are unnecessary but since the extent of range is not known till after the trapping, the distances will have to be measured anyhow.

Data of the recapture type for man were obtained from a traffic survey in Baltimore in 1945–1946 (Table 4). The details are recorded in "Report of the Transportation Study, Baltimore Metropolitan Area, Volume II, Traffic Flow

Tables", published by the State of Maryland Roads Commission. The data were collected by interview of 5 per cent of the homes and 20 per cent of the truck drivers and taxi-cabs in the city. The accuracy of the results of interviews was

TABLE 4.—*Distance of movement of Homo sapiens*

MIDPOINT OF DISTANCE IN MILES	A NUMBER OF TRIPS	B NUMBER OF DISTANCES	A/B	C PER CENT	D PER CENT OF A/B WITHIN	E PER CENT OF A WITHIN
0.01	4970	44	113	10.9		
0.44	8808	95	93	8.9		
0.88	14989	103	146	14.0		
1.32	20787	152	137	13.1		
1.76	16643	174	96	9.2		
2.20	11042	158	70	6.7	62.7	48.4
2.64	10881	184	59	5.7		
3.08	12445	234	53	5.1		
3.52	8882	190	47	4.5		
3.96	7782	266	29	2.8		
4.40	7591	293	26	2.5	83.2	78.2
4.84	6356	260	24.4	2.34		
5.28	6788	266	25.5	2.45		
5.72	4512	249	18.1	1.73		
6.16	4675	256	18.3	1.75		
6.60	2989	252	11.7	1.11	92.6	94.1
7.04	2463	228	10.8	1.03		
7.48	2332	205	11.4	1.09		
7.92	1608	144	11.2	1.07		
8.36	1200	128	9.4	.90		
8.80	515	114	4.5	.43	97.1	99.2
9.24	448	81	5.5	.53		
9.68	210	68	3.1	.30		
10.12	167	51	3.3	.31		
10.56	146	42	3.5	.33		
11.00	80	33	2.4	.24	98.8	99.9
11.44	52	35	1.5	.14		
11.88	45	20	2.3	.22		
12.32	21	8	2.6	.25		
12.76	45	10	4.5	.43		
13.20	0	1	0	0	100	100
13.64	0	3	0	0		
Totals	159472	4347	1043.0			

checked by actually counting the number of cars passing three different places in the city. The predicted values were within 9, 12, and 12 per cent of the actual values. The questions asked obtained data about the places visited during an

average week day. These places were recorded according to zones, and hence the number of trips within and between zones could be determined. The distances between zones varied with the size and location of the zone. It should be noted that, since unusual or weekend trips are excluded, these data are better than those for most other mammals because transients are omitted. Table 4 presents the data in some detail. Since the frequency of the distances between zones (traps) was unequal it is necessary to divide the number of trips of a given distance by the number of such distances available, to get comparable values. These ratios are given in the column headed A/B. For example, note that although the number of trips in the classes 0.44 miles and 3.52 miles was about the same, the number of opportunities to record trips of 3.52 miles was twice that for 0.44 miles. This correction is important when there is a great difference in the number of distances available. Compare, in Table 4, column D, which gives, within certain distances, the percentage of trips divided by the number of distances (A/B) and, on the other hand column E, which gives merely the percentage of trips (A). The small number of short distances between "traps" permits column E to give a false impression that 48.4 per cent of the trips were within 2.20 miles whereas a more true picture is given by column D with 62.7 per cent within 2.20 miles.

The synthetic model emphasizes some aspects of interpretation of recapture data. The data in Table 1 include dispersants as well as rats that remained within their home range, and there seems to be no way of distinguishing between them. Some arbitrary distance (126 feet) may be chosen empirically. It must be recognized that the number of recaptures at this (or any limiting distance) greatly underestimates the frequency of movement of these distances. Furthermore, the model suggests that the data in Table 1 underestimate the short movements because the number of chances of capture at a short distance is much less than the number at long distances.

This model, of course, is not a duplication of natural conditions and has some obvious defects which need not be listed here. It does, however, call attention to likely deficiencies in the interpretation of recapture data. But the problem is that there are species that cannot be recaptured frequently, whose home ranges we need to understand. Trapping in a grid, of course, overcomes many of these deficiencies but is useless for species that can rarely be recaptured. Perhaps the only way to determine the home range of such mammals is to observe them directly, as can be done with birds. Such observations are difficult, but perhaps attention should be devoted to development of technics rather than to the accumulation of dubious recapture data.

An empirical relationship has been noticed between the frequency of recaptures and the distances. When plotted on double logarithm paper a straight line results. A mathematical model that represents this relation is $fr^x = c$, or $\log f + x \log r = \log c$, which is a straight line of negative slope x. f represents frequency of recapture, r represents distance, and c is a constant. This line descends and then sharply bends toward the r axis ($f = 0$). The value of r at the place of the bend may be related in a constant manner to the size of the home range, but until carefully collected data are available the relationship cannot be generalized.

SUMMARY

Analysis of movements and home ranges of vertebrates is difficult for species that can rarely be recaptured or that travel long distances. The usual methods of grid-trapping are inapplicable. Analysis of distances between captures is illustrated by data for 2792 recaptures of Norway rats (*Rattus norvegicus*) and 159,472 recaptures of Baltimoreans (*Homo sapiens*). This method has several biological and statistical deficiencies. An improvement is to divide each frequency of recapture by the number of opportunities for recapture at that distance. It is recognized that direct observation may be the only suitable method for some species.

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STATUS OF THE FOX SQUIRREL IN NORTHEASTERN COLORADO

By Robert L. Hoover and Lee E. Yeager

It is well known that many, if not most, mammals tend to extend their range under conditions of suitable environment and favorable climate in adjacent, unoccupied territory. The coyote is perhaps the outstanding current example of such extension of range among common American mammals (Young and Jackson, 1951). Another of the numerous species to extend its original range is the fox squirrel, *Sciurus niger*. This animal has moved principally to the north and west from its ancestral distribution in the midwestern states (Bailey, 1929; Seton, 1937; Allen, 1943). In miles, the greatest distance has undoubtedly been to the west. This paper gives the present status of the western fox squirrel, *S. n. rufiventer*, in the South Platte River drainage of northeastern Colorado, on range that appears to have been added both through stocking and westward invasion.

This is a contribution of the Colorado Cooperative Wildlife Research Unit, Colorado A & M College, Fort Collins; the Colorado A & M College, the Colorado Game and Fish Department, the Wildlife Management Institute, and the U. S. Fish and Wildlife Service, cooperating. Grateful acknowledgment is made to Professor J. V. K. Wagar of Colorado A & M College for partial supervision of this project and for numerous suggestions relative to field work and report preparation.

Methods.—Although field work was relatively rapid, it is believed that coverage was sufficiently detailed to give reliable information on the distribution, economics, and population trends of the fox squirrel in the valley. The grid system of public roads, usually along section lines, facilitated automobile travel; and the pronounced tendency of farmers to live close to these roads facilitated inquiry. In general, the entire valley was covered in a series of north-south transects west of U. S. 87, and east-west transects east of this road. All transects were at one- to three-mile intervals. Where access roads were lacking, any necessary travel was done on foot. Field work required 335 hours and 6,480 miles of automobile travel; it was begun in January and completed in May, 1951.

Records were taken systematically, by kind and locality, through the 13-county area involved. Sixty animals were sighted, 563 nests observed, 11 specimens collected, and nine squirrel cuttings or other indisputable signs of their presence were found. Out of 579 resident contacts there were 372 positive, and 207 negative, reports on the presence of fox squirrels. Resident contacts included rural and urban people, game wardens, students, and others. The total number of direct and indirect records was 1,015.

OBSERVATIONS

Distribution.—The present range of the western fox squirrel in northeast Colorado is shown in Figure 1.

During the survey considerable attention was given to the collection of stocking records,

in order to ascertain the relative importance of stocking vs. natural spread (invasion) in attaining the present status of this squirrel in northeastern Colorado. Out of 579 resident contacts, eight apparently reliable stocking records were obtained. Dates of stocking usually could not be recalled with certainty; one near Greeley (about half-way along the east-west axis of the South Platte drainage) was prior to 1908. Here, squirrels from Omaha were released. Another, near Sterling, was about 1921, and a third, at Fort Collins, was prior to 1927. It appears that an appreciable, though unknown, number of plants were made at various points throughout the Valley, mostly by persons who had known the fox squirrel in more eastern states. Cary (1911) states that this species is ". . . not indigenous to Colorado, but has been introduced at Greeley, where they are increasing in a gratifying manner . . ." A similar observation (Young, 1908) recorded their increase at Denver. It seems reasonably certain that, while stocking was instrumental in establishing the fox squirrel in the plains

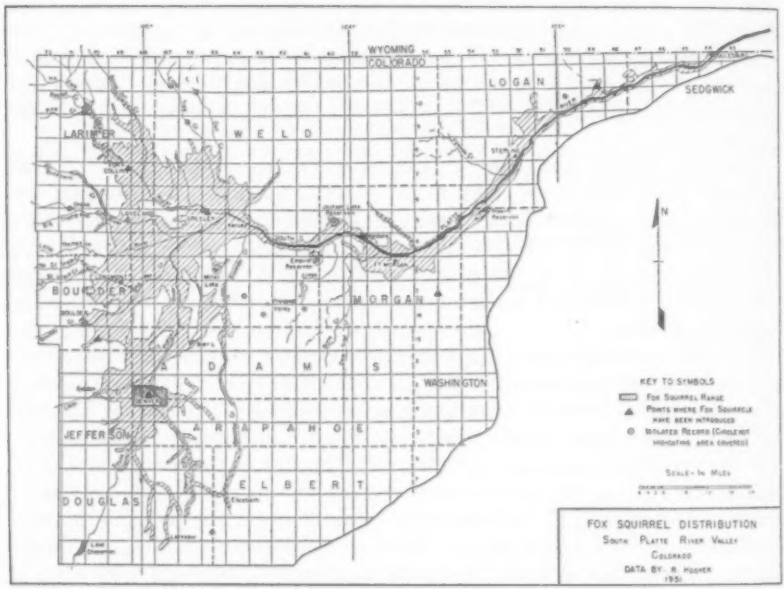

FIG. 1.—Fox squirrel distribution, north-central and northeastern Colorado, 1951.

portion of the South Platte drainage in Colorado, natural invasion played some part. The fox squirrel is native to Nebraska, Seton's (1937, 4: 85) distribution indicating their occurrence along the Platte in that state.

Even to the casual observer, the only range originally habitable to fox squirrels in northeast Colorado was the wooded bottoms of the South Platte and its tributaries. Extensive development of irrigation since about 1880 and, to a lesser extent, the planting of shade trees in towns has added to the bottomland range. Fox squirrels now inhabit the rows of cottonwood trees which often border irrigation ditches, sometimes several miles from the Platte Valley.

One distribution record is worthy of special notice, since it extends the range of the fox squirrel to its westernmost point in the South Platte drainage. This animal was shot by a timber cutter in February, 1952, on Buckhorn Creek, about 20 miles west of Fort Collins from the scraggy cottonwoods growing along the stream, at an elevation of about 7,800

feet. The forest type in this locality is ponderosa-lodgepole pine. This record was obtained by Ralph W. Meeks (unpublished), a student at Colorado A & M College. Meeks had previously observed fox squirrels on the Buckhorn a few miles east of this point; and the senior author, during field work in March, 1951, learned at their presence in the locality. This is believed to be a case of gradual invasion up the Buckhorn, a tributary of the Big Thompson River, which, in turn, empties into the South Platte about eight miles southwest of Greeley. Cultivated land, usually meadow but sometimes grain, and always in small patches, occurs along the smaller streams to within a few miles of this site.

In the extensive area occupied by squirrels immediately east of the Continental Divide, several sizable "islands" are uninhabited, due to lack of irrigation, and, therefore, tree cover.

Area.—From its emergence onto the high plains to the eastern Colorado boundary, the South Platte River traverses nearly one-half of the east-west length of the state, or about 200 miles. The valley, only a few miles wide for about two-thirds of its Colorado length, suddenly expands at Kersey due to the confluence of several streams flowing off the Continental Divide some 50 miles to the west (Fig. 1). Along the foothills bounding the western extension of the valley proper, the South Platte and its tributary system attain a width (actually north-south length) of about 120 miles. The total area, including both the valley and contiguous irrigated land—all of the territory offering the possibility of irrigation, and hence tree-squirrel occurrence—is roughly 2,400 square miles.

Cover.—In Figure 1, the ribbon-like pattern of fox squirrel distribution along the South Platte, and the blocked-out pattern in the extensive irrigated region immediately east of the mountains, is shown graphically. The tree cover delimiting this area—a direct water relationship—consists chiefly of cottonwood (*Populus sargenti*) and willow (*Salix* spp.), with an occasional box elder (*Acer negundo*) in the composition. In towns, elms (*Ulmus* spp.), maples (*Acer* spp.), ash (*Fraxinus* spp.), and occasional trees of other kinds, provide some variety. The principal shrubs are rose (*Rosa fendlei* and *R. arkansana*), snowberry (*Symphoricarpus* sp.), and sand cherry and wild plum (*Prunus* spp.) on irrigated areas. Wild grapes (*Vitis* spp.) occur as far west as Fort Collins, and brambles (*Rubus* spp.) are common. Forbs grow luxuriantly in the absence of grazing, the dominant species being wild sunflowers (*Helianthus* spp.) and cockleburs (*Xanthium* spp.).

In marshes, cattail (*Typha* sp.) and bulrushes (*Scirpus* spp.) predominate; cordgrass (*Spartina* sp.) is the chief vegetation of permanently moist, unshaded bottoms; and saltgrass (*Distichlis* spp.) becomes the chief cover on drier, alkaline bottoms. Shrubs, forbs, and grasses, in varying combinations, produce dense ground cover where ungrazed. A very considerable portion of bottomland, and often ditchbanks, are grazed, especially in winter.

Cottonwoods and willows, especially along the larger streams provide, according to age, thin to excellent cover, including den cavities, for squirrels. A typical mature cottonwood stand averages 14 usable cavities per acre. Many stands, particularly along ditches, are younger and of course less dense. Young cottonwood trees lack cavities, thus providing inferior cover. Willows, often aged and decadent, occur along stream banks and in swales and provide additional cavities. Leaf nests are common, cottonwood leaves evidently offering good material for construction.

Food.—Grain agriculture in immediate proximity to the cottonwood-bordered streams or bottoms provides the basic food source for fox squirrels. There is general evidence to suggest that the western movement of this species followed settlement and grain farming, thus indicating that the lack of suitable food was one of the principal reasons why fox squirrels were not indigenous to Colorado.

Burkholder (1949), a student at Colorado A & M College, determined the winter foods of a series of squirrels taken in the Fort Collins vicinity. The junior author has kept records of fox squirrel foods over a four-year period. The combined data are presented in Table 1.

It is evident that the findings reported in part II of Table 1 support the more careful work of Burkholder, given in part I. In both studies, grains clearly constituted the bulk of the diet during the fall and winter. The junior writer found wheat and oats in addition to barley

and corn, and found that corn ranked first in quantity eaten. Most of his collections were near cornfields. Clearly, fox squirrels take the grain available in the vicinity of their home range. Buds, principally of cottonwood, but at times including those of elm, box elder, and maple (especially in towns), may be considered the only other staple winter food, their occurrence in the diet being more frequent in January and February than during the fall. Presumably, grains, which are generally abundant, take the place of nuts, acorns, and other mast, totally lacking in this region. A wide variety of miscellaneous foods are eaten.

TABLE 1.—*Fall and winter foods of fox squirrels, north-central Colorado*

I—Burkholder (1949): 23 animals*

FOODS	OCCURRENCE		DRY WEIGHT	
	Number	Per cent	Grams	Per cent of weight
Barley	11	47.2	105.16	71.7
Corn	10	43.5	15.53	10.6
Buds and bark (mostly cottonwood)	3	13.1	4.84	3.3
Wild plum	1	4.4	6.70	4.6
Potato (pulp)	1	4.4	3.51	2.4
Meat (muskrat, bird, fish?)	1	4.4	3.05	2.1
Apple (seeds and pulp)	1	4.4	2.85	1.9
Ragweed	1	4.4	2.26	1.5
Sugar beet (pulp)	1	4.4	1.50	1.0
Unidentified (insects, vegetation)	—	—	1.35	0.9
Total	—	—	146.75	100.0

II—Yeager (1948–52): 78 animals

CONSUMPTION (FOODS RANKED ACCORDING TO VOLUME PRESENT IN STOMACH)	NUMBER OF STOMACHS BY FOOD GROUPS					
	Grains	Buds	Fruits	Sugar beet	Insects	Miscellaneous
First (10 stomachs empty)	48	13	2	1	0	4
Second (10 stomachs with only 1 food)	14	12	19	2	0	11
Third (17 stomachs with only 2 foods)	7	15	9	0	2	18
Fourth (18 stomachs with only 3 foods)	4	11	16	?	5	14

* Unpublished report, Colo. Coop. Wildlife Research Unit, Colorado A & M College. Fort Collins, Colorado.

Authentic cases of fox squirrels eating cockleburs were obtained. The first, February 10, 1951, was a time of deep snow, when two animals living in the Cache la Poudre bottoms near Windsor, Colorado, were flushed in a cocklebur patch. Examination showed numerous freshly shelled hulls and, of course, tracks; later observations on this date disclosed actual feeding on cockleburs. Harold M. Swope of the Colorado Game and Fish Department has numerous records, all during winter months, of fox squirrels feeding on cockleburs near Crook, Colorado. Use of this food may point to the shortage, or at least unavailability, of grain or other staples during periods of heavy snow.

The foods utilized during the late winter, spring, and summer were not studied quanti-

tatively. Based on numerous observations, however, grain residues, buds, catkins, and elm and maple seeds (in towns) are the standbys until about mid-June, when early fruits and berries become available. The abundance of fruits, plus unripened grain, insures against food contingencies during the summer season.

Since squirrels are limited to wooded bottoms and irrigation ditches, water during the spring and summer is seldom a problem. However, when irrigation ceases, usually in September, and ditches dry up, squirrels situated at some distance from live streams may suffer for lack of water if succulent foods are not available. The frequency with which fox squirrels were reported drowning in stock watering tanks emphasizes this possibility. Practically all range along the South Platte River proper is amply watered.

Damage.—In the 372 positive contacts made in the field, only 54, or less than 15 per cent, reported damage of any sort. Most complaints were by farmers who listed minor crop and orchard losses, eating of chicken feed and eggs, and gnawing into buildings. Urban complaints were confined to house entering, fruit eating, and cutting off shade tree branches. Fifteen reports were received from farmers and others who stated that squirrels shorted transformers by gnawing or other activity.

Interest in control was confined largely to city residents and powerline users. Farmers, generally, accepted squirrel damage as a matter of course, and occasionally shot offending animals. A majority of the rural residents contacted stated that they liked to have squirrels around; some did not permit hunting of them on their property. It is evident that the fox squirrel as a species does not constitute a serious damage problem in northeastern Colorado.

Reproduction.—The breeding season of fox squirrels has been reported in detail by Baumgartner (1940), Allen (1943), and Brown and Yeager (1945). Limited work by Burkholder (unpublished report) indicated general similarity in time of breeding in Colorado as compared to Michigan and Illinois. In the 16 females handled by Burkholder, January 8 to March 3, 1949, six appeared to be sexually inactive; six, taken January 13 to February 24, were in oestrus; and four (February 3 to March 3) were pregnant. Copulation was observed on January 26.

The peak in pregnancy appeared to occur early in March, whereas, in Illinois, this event was recorded early in February (Brown and Yeager, 1945; 475). This findings indicates the main breeding season in Colorado to be three or four weeks later than in Illinois. The peak of mating would, therefore, occur late in January; in Illinois, it occurred during the period of December 15 to January 15. The later reproductive period is presumably due to the colder Colorado climate.

All squirrels taken in Colorado live in close proximity to grain fields. It is interesting that the nine sets of embryos taken in Colorado animals should closely approximate the average for 75 sets from farmland squirrels in Illinois, the figures being 3.66 and 3.40, respectively (*op. cit.*: 489).

In the small Colorado sample of 128 fox squirrels, 70 males and 58 females, the sex ratio was 121 males: 100 females. All were taken by hunting. The Illinois figure for 2,749 fox squirrels shot by hunters during seasons that began July 15, was 146:100 (*op. cit.*: 458). Baumgartner (1938: 688) noted a sex ratio of 124:100 in 954 Ohio fox squirrels taken during the open season of 1937 (September 25 to October 10). He reported that the highest percentage of males was handled during August and September; the lowest in October.

Hunting.—Unlike most other parts of the country, squirrel hunting pressure in northeastern Colorado is comparatively light. Many landowners protect squirrels, particularly in homestead groves. It is believed that the relative abundance of big game, waterfowl, pheasants, and cottontail rabbits, in addition to fall harvest responsibilities, serve to reduce interest in squirrels. Indeed, the average hunter is under the impression that they are protected, since the species is not mentioned in the Colorado game laws. In reality, it is an unprotected species and may be hunted legally at any time. It is believed by the Colorado Game and Fish Department, and concurred in by the writers, that omission of fox squirrels from the regulations actually gives greater protection than if they were listed as huntable game. This policy may need revision in the event of increased pressure, for obviously no

species as easily hunted and as restricted in distribution as the fox squirrel in Colorado can withstand the toll of hunters in present-day numbers.

The heaviest squirrel hunting probably occurs in the vicinity of Fort Collins, where a number of A & M College students from more eastern states pursue a sport with which they are familar. That hunting may be good in this locality is attested by frequent individual bags of four or five squirrels for less than a half-day afield. Few regions east of Colorado yield comparable kills on a sustained basis.

SUMMARY

The western fox squirrel, absent in the original Colorado fauna, now occurs along 200 miles, and on about 2,400 square miles, of the South Platte River drainage and contiguous irrigated land in northeastern Colorado. Both stocking and natural invasion from the east appear to be involved in this extension of range.

Distribution is delimited by the occurrence of trees, almost entirely cottonwood and willow, along streams and ditches, and a variety of hardwoods in towns. Irrigation has appreciably enlarged the original habitable range. Grain agriculture adjacent to tree cover completes the habitat by supplying a dependable source of winter food. Barley, corn, wheat, and oats constitute at least 75 per cent of the winter diet. It seems probable that the development of grain farming was concurrent with the greatest western invasion of the species. A variety of miscellaneous foods, among which buds are important, are taken. Water does not limit the habitat except for squirrels living on irrigation ditches, and here only after cessation of flow late in summer.

Less than 15 per cent of 372 persons reporting the presence of squirrels complained of damage. Complaints involved a variety of crops, poultry feed, eggs, gnawing into buildings, and short-circuiting of electrical transformers. Requests for control were largely restricted to urban residents and power-line users. Many farmers protect squirrels around their homesteads.

The breeding season in Colorado fox squirrels appears to be three or four weeks later than in Illinois, presumably due to the colder climate. Embryo counts averaged 3.66 as compared to 3.40 in grain-fed fox squirrels in Illinois. The sex ratio in 128 Colorado animals was 121 males to 100 females.

Hunting pressure is comparatively light in Colorado, despite the non-game, and, therefore, unprotected status of the fox squirrel in this state.

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STUDIES ON RAT REPRODUCTION IN SAN FRANCISCO

BY TRACY I. STORER AND DAVID E. DAVIS

Despite the almost universal presence of introduced rats (of the genus *Rattus*) in the cities of the temperate and tropical portions of the world, there is a paucity of detailed information concerning their biology. The relative abundance of the two species (*Rattus rattus* and *R. norvegicus*) is not well known, and there are only a few detailed accounts of their breeding rate. Efforts at control are often ineffective through failure to know or to appreciate their habits.

For a number of years the United States Public Health Service and the Department of Public Health of the City and County of San Francisco cooperatively trapped and examined upwards of 20,000 rats annually in a watch for plague. This provided an opportunity to gather relevant facts concerning the biology of the two species of rats. Through the kindly interest of Senior Surgeon J. C. Perry and Surgeon N. E. Wayson of the Public Health Service, arrangements were made, in 1925, to gather data on the general size and number of embryos present in the animals being examined. This record continued from July 1, 1925 to June 30, 1927 and from January 1 to December 31, 1928. In 1926–27 through financial assistance granted by Dr. William C. Hassler, Health Officer of San Francisco, part time help was available from October 1, 1926, until September 30, 1927, to measure and weigh specimens. A grant (Agriculture No. 278) from the Research Board of the University of California, provided a Toledo scale for rapid weighing of specimens. To these organizations and persons, and especially to Dr. Wayson and his laboratory helpers and particularly Mr. Earl M. Tennis, for their sympathetic interest in a problem that was wholly additional to their routine duties, we are grateful for the aid rendered in gathering the raw data. The Surgeon General of the Public Health Service has granted permission to publish the data.

The rats were trapped by a crew of five or more men working chiefly in the eastern (commercial) portion of the city about slaughter houses, food-stuff warehouses, restaurants, hotels, and apartment houses. A small percentage of animals was discarded because of damage by traps, but no conscious effort was made to catch individuals of particular size, sex, or age, so that the trapped rats are as

near a "random" sample as could be obtained under the conditions stated. Traps were set and baited one day and were visited the following day. The rats were taken to the laboratory where they were examined the following morning. Thus at least 24 hours, and, in some cases, more time elapsed between capture and examination.

In order to determine the effect of delay on the weights and measurements, a series of live specimens of *norvegicus* were chloroformed, measured, and weighed immediately after death, and then weighed at intervals of 24, 48, and 72 hours, respectively. The results indicate that the differences are never as much as five per cent, and may be less.

TABLE 1.—*Relation of weight to head and body length of rats*[1]

MIDPOINT OF LENGTH CLASS	RATS MEASURED		MEAN WEIGHT		STANDARD DEVIATION	
	Male	Female	Male	Female	Male	Female
			Norway Rats			
95 mm.	27	30	41.0 gm.	48.7 gm.	36.2	44.0
125	568	1558	60.6	58.0	23.2	12.8
155	675	1699	88.7	87.4	23.1	9.6
185	602	1574	153.7	156.7	35.9	32.0
215	1080	1848	241.9	247.6	43.9	49.0
245	1336	1200	355.1	341.4	58.6	62.5
275	182	67	426.9	375.0	58.6	123.1
			Roof Rats			
100 mm.	84	139	28.1 gm.	30.3 gm.	10.0	10.0
120	239	264	42.5	43.1	2.2	11.7
140	159	158	65.3	65.7	11.8	15.4
160	119	141	80.2	101.8	17.7	20.6
180	175	210	142.6	142.8	24.4	26.5
200	142	193	176.1	189.1	28.8	32.0

[1] The rats are not a random sample of trapped rats and must *not* be used to calculate mean weight of each sex, or sex ratios.

In San Francisco, both species are present and both "subspecies" of roof rats are found (the three year totals being 9,062 for *Rattus r. rattus* and 11,523 for *R. r. alexandrinus*). In San Francisco, Norway rats were at ground level, and roof rats above ground (or paradoxically, in basements "rat-proofed" against Norway rats!). In general, Norway rats seemed more abundant than roof rats, although the gross totals do not necessarily express the numerical relations. Differences in the places where the traps were set influenced the relative numbers of each species obtained.

In order to standardize the measurements, a device was constructed on which the rat was stretched at full length with a loop of wire hooked about the incisor teeth to hold the head in position. A clamp, with a cord that led over a pulley to a 200 gram weight, was attached to the tail. With the specimen at uniform tension the total length was measured from the tip of the nose (specimens with skulls badly crushed were discarded) to the end of the tail vertebrae. A some-

what similar arrangement, with the tail bent at 90 degrees and a tension-weighted clamp, was used to measure the length of the tail vertebrae. Lengths (Tables 2, 3) refer to total length, i. e., from tip of snout to tip of tail. In the early part of the study the weights were obtained on a Troemmer balance read to the nearest 0.2 ounce and converted to metric equivalents; later a Toledo self-registering scale, reading to about two gram divisions was used.

Because of limitations of time, only part of the rats was examined each day. The large females and the large males were recorded, and then as many small individuals as time permitted. Thus these data must *not* be used for calculations of mean weight, mean length, or sex ratio of the population. Proportional calculations such as per cent pregnant are, of course, valid, and are developed here.

Data for the relation of weight to total length are given in Table 1. These detailed measurements were obtained only in 1927. Note that, since the data are not a random sample of trapped rats, sex ratios and mean weights of all rats would refer only to "examined rats" and hence are biologically meaningless. The data in the table show that males and females of both species have about the same weight at a given length and also rats of both species have the same weight for a given length. When plotted on a graph the points overlap so consistently that the graph is not readable and hence not presented. The line for both sexes of both species bends gradually showing that the relative gain in weight is greater than the gain in length.

Reproductive activity.—The prevalence of pregnancy among the large (i.e., over 14 inches, total length) female Norway rats (Table 2) shows a semi-annual fluctuation in the three annual records obtained. One peak occurs about September and another about May. The changes in prevalence of pregnancy in roof rats do not show regular seasonal variation (Table 3). The ecologic differences in habitat characterizing these two species must be emphasized. The Norway rat is characteristically a rat of the ground floor in multi-storied buildings, and is thus more exposed to fluctuations in climatic conditions than the roof rats, which live in the more evenly regulated temperature of hotels and apartment houses. Weather bureau records in San Francisco are unfortunately taken at the 15th story level instead of at the ground level where most human beings and the Norway rat population live and hence are useless for our purpose. Nevertheless there is a slight rise in the monthly means of temperature, both maximum and minimum, in spring and autumn, but it scarcely seems adequate to explain the striking fluctuations in breeding activity. In San Francisco the winters are mild, the summers are cooled by ocean fogs, and sunny days and mild nights are commonest in spring and autumn. The winter temperature means in San Francisco drop considerably, but the midsummer means are not depressed significantly.

The number of embryos (visible macroscopically) per pregnant female is recorded in Table 2 for Norway rats and Table 3 for roof rats. For both species there was considerable variation from month to month, but no regular seasonal trends are apparent. The relation of the number of embryos to their size (Table 4) shows that there was some resorption in Norway rats since there were signifi-

TABLE 2.—*Reproductive data for Norway rats examined in San Francisco, 1925–1928*

		LARGE (OVER 14 INCHES)						MEDIUM (12-14 INCHES)					
		Rats		Pregnant ♀		Embryos		Rats		Pregnant ♀		Embryos	
		Males	Females	Total	%	Total	Mean	Males	Females	Total	%	Total	Mean
1925	July	381	399	62	15.5	515	8.3	203	208	12	5.7	87	7.2
	Aug.	226	191	40	20.9	365	9.1	186	195	10	5.1	79	7.9
	Sept.	322	366	105	27.7	978	9.3	129	218	28	12.8	201	7.2
	Oct.	357	417	118	28.3	1092	9.3	214	279	22	7.8	162	7.4
	Nov.	358	352	65	18.4	594	9.1	218	288	11	3.8	78	7.1
	Dec.	409	400	52	13.0	452	8.6	263	300	5	1.7	26	5.2
Totals		2052	2125	442	19.1	3996	9.0	1213	1488	88	6.7	633	7.2
1926	Jan.	454	421	61	14.4	530	8.6	159	164	2	1.	12	6.0
	Feb.	395	430	80	18.6	737	9.2	186	170	3	1.	20	8.3
	Mar.	414	494	98	24.8	898	9.1	142	160	1	.03	8	8.0
	Apr.	338	369	108	29.2	956	8.8	164	172	10	5.8	68	6.8
	May	280	260	86	33.0	773	8.98	141	159	12	7.5	80	6.6
	June	300	261	65	24.9	610	9.38	193	229	24	10.5	175	7.3
	July	285	254	45	17.7	429	9.54	188	225	15	6.7	102	6.8
	Aug.	367	321	44	13.7	348	7.91	326	425	25	5.9	184	7.36
	Sept.	303	340	63	18.5	596	9.46	135	160	2	1.3	14	7.0
	Oct.	335	407	64	15.7	601	9.39	164	196	2	1.	12	6.0
	Nov.	335	344	46	13.4	369	8.02	165	158	1	0.6	7	7.0
	Dec.	372	399	37	9.3	305	8.24	123	137	—	x	—	x
Totals		4178	4300	797	19.5	7152	9.0	2086	2355	97	3.5	682	7.0
1927	Jan.	342	326	56	17.3	471	8.41	118	200	6	3.	41	6.8
	Feb.	353	279	67	24.0	612	9.13	139	200	5	2.5	31	6.2
	Mar.	444	452	111	24.6	1030	9.28	105	130	8	6.	50	6.2
	Apr.	400	407	128	31.4	1162	10.31	134	164	6	3.7	38	6.2
	May	406	414	135	32.6	1261	9.34	71	121	4	3.3	24	6.0
	June	382	437	100	22.9	849	8.49	142	126	5	4.0	30	6.0
Totals		2327	2415	597	25.4	5385	9.0	709	941	34	3.8	214	6.3

	June	382	457	100	22.9	849	8.49	142	126	3	4.0	30	6.0
Totals		2327	2415	597	25.4	5385	9.0	709	941	34	3.8	214	6.3
1928	Jan.	222	218	17	7.8	161	9.47	20	42	—			
	Feb.	434	400	78	19.5	689	8.83	62	79	0			
	Mar.	498	469	102	21.7	968	9.49	92	118	2	1.7	12	6.0
	Apr.	411	383	113	29.5	1040	9.21	92	107	10	9.4	61	6.1
	May	412	469	139	29.6	1198	8.62	1128	133	7	5.3	46	6.5
	June	307	327	91	27.8	676	7.43	109	155	16	10.3	103	5.5
	July	324	295	53	17.9	507	9.57	83	104	2	2.0	11	5.5
	Aug.	409	368	74	20.1	688	9.30	106	141	2	1.4	16	8.0
	Sept.	478	333	92	27.6	862	9.37	96	120	2	1.7	9	4.5
	Oct.	388	380	71	18.6	679	9.56	125	143	3	2.1	20	6.6
	Nov.	389	335	44	13.1	375	8.52	133	148	6	4.1	36	6.0
	Dec.	392	348	58	16.6	541	9.32	128	146	1	0.7	5	5.0
Totals		4564	4325	932	21.2	8385	9.0	1174	1436	51	3.2	319	6.3
Grand totals		13124	12962	2768	21.3	24918	9.00	5182	6220	270	4.34	1898	6.84

TABLE 3.—*Reproductive data for roof rats examined in San Francisco, 1925–1928*

		LARGE (OVER 15 INCHES)						MEDIUM (13–15 INCHES)					
		Rats		Pregnant ♀		Embryos		Rats		Pregnant ♀		Embryos	
		Males	Females	Total	%	Total	Mean	Males	Females	Total	%	Total	Mean
1925	July	40	64	24	37.5	130	5.4	17	34	0			
	Aug.	56	41	5	12.1	39	7.8	32	32	1		8	
	Sept.	56	58	22	37.9	163	7.4	28	42	4		25	
	Oct.	108	79	23	29.1	166	7.2	54	66	4		20	
	Nov.	129	167	53	31.7	370	7.0	82	83	6		33	
	Dec.	221	294	71	24.1	479	6.7	117	114	6		36	
Totals		610	703	198	28.9	1347	6.8	330	371	21	5.7	122	5.8
1926	Jan.	134	135	37	27.4	271	7.3	64	59	1		5	
	Feb.	132	115	36	31.3	274	7.6	39	63	1		5	
	Mar.	156	168	39	23.2	287	7.4	65	62	0		0	
	Apr.	145	164	34	20.7	259	7.9	50	56	7		38	
	May	111	126	46	36.5	331	7.2	43	30	4		28	
	June	117	133	30	22.5	192	6.4	61	69	9		57	
	July	139	120	36	30.0	262	7.3	71	70	14		67	
	Aug.	118	116	21	18.1	134	6.4	60	93	6		34	
	Sept.	111	103	29	28.1	233	9.0	41	54	3		12	
	Oct.	126	99	22	22.2	149	6.8	32	41	0		0	
	Nov.	96	93	17	23.6	118	6.9	45	52	2		10	
	Dec.	82	86	15	17.4	104	6.9	40	41	2		14	
Totals		1467	1458	362	25.1	2614	7.3	611	690	49	7.1	270	5.5
1927	Jan.	62	94	29	30.8	220	7.6	33	50	2		12	
	Feb.	137	146	56	38.3	440	7.9	64	48	4		27	
	Mar.	148	146	48	32.3	375	7.8	76	60	4		25	
	Apr.	87	86	26	30.2	194	7.5	62	58	6		29	
	May	69	63	23	36.5	173	7.5	42	32	3		14	
	June	71	86	25	29.0	201	8.0	66	46	5		26	
Totals		574	621	207	32.9	1603	7.8	343	294	24	8.2	133	5.5
1928	Jan.	49	33	4	12.1	27	6.7	26	26	3		18	
	Feb.	61	64	14	21.8	120	8.6	21	31	4		24	
	Mar.	83	59	9	15.2	73	8.1	33	38	1		6	
	Apr.	88	81	31	38.2	237	7.6	46	37	4		24	
	May	90	97	35	36.0	269	7.7	33	28	4		20	
	June	114	87	23	26.4	148	6.4	23	48	2		11	
	July	41	25	5	20.0	35	7.0	8	17	1		6	
	Aug.	106	96	23	23.9	195	8.5	52	36	2		14	
	Sept.	81	52	14	26.9	123	8.8	33	27	1		4	
	Oct.	75	88	16	18.1	122	7.6	40	36	0		—	
	Nov.	69	53	12	22.6	86	7.2	27	27	1		7	
	Dec.	118	116	25	21.5	206	8.2	47	42	1		7	
Totals		975	851	211	23.5	1641	7.8	389	393	24	6.1	141	5.9
Grand totals		3626	3633	978	26.9	7105	7.3	1673	1748	118	6.7	666	5.6

cantly fewer (P = .05) large embryos than small embryos. Such a relation is not apparent for roof rats.

The length of rats in relation to prevalence of pregnancy was studied during most of the year 1927. Table 5 gives detailed measurements showing that prev-

TABLE 4.—*Relation of size of embryo to number per pregnant female*

SIZE OF EMBRYOS	NORWAY RATS	ROOF RATS
Small		
Pregnant rats	358	60
Mean embryos	9.1	7.8
Standard error	0.12	—
Medium		
Pregnant rats	245	62
Mean embryos	8.9	7.0
Standard error	0.13	—
Large		
Pregnant rats	200	30
Mean embryos	8.6	7.3
Standard error	0.15	—

TABLE 5.—*Relation of head and body length of rat to prevalence of pregnancy, 1927*

MIDPOINT OF LENGTH (MM.)	FEMALES	PER CENT PREGNANT	EMBRYOS	
			Mean	Standard Error
		Norway rats		
125	2354	0.4	—	—
175	2625	1.9	6.6	0.29
225	3620	21.3	8.9	0.07
325	14	28.6	11.5	1.14
375	2	100.0	—	—
Total	9006	10.4	8.9	0.07
		Roof rats		
155	3	14.3	6.7	—
165	7	21.9	6.0	1.3
175	31	97.0	6.3	1.6
185	34	89.5	6.9	1.5
195	38	74.5	9.4	2.1
205	33	75.0	8.1	2.4
215	11	64.0	8.1	1.7
225	0	—	–	–
235	3	100	8.0	–

alence increased with the length of Norway rats and with length of roof rats. The number of embryos also increased for both species (Table 5). However, a detailed analysis of the data shows a correlation coefficient for number of embryos and length of rat to be only + 0.29 for Norway rats and + 0.22 for roof rats, which indicate little significance. Data (Table 6) for weight in relation to

pregnancy shows a positive correlation. There is a great difference, due to the large number of small rats, between the weighted percent (total pregnant divided by total females) and the standardized percent (sum of per cents divided by 12).

The number of pregnancies during a year may be calculated from the prevalence of pregnancy by the formula: $I = 365P/18$ where I is incidence of pregnancy, P is prevalence of pregnancy, 365 is the number of days in a year, and 18 is the number of days during which pregnancy can be observed macroscopically. Table 7 gives the results of calculations utilizing the data in Tables 2 and

TABLE 6.—*Relation of weight of rat to prevalence of pregnancy in Norway rats, 1927*

MIDPOINT OF WEIGHT CLASS	TOTAL FEMALES	PER CENT PREGNANT
105 gm.	990	0.3
145	873	1.2
185	829	5.2
225	842	12.6
265	832	20.2
305	686	27.5
345	592	27.4
385	399	30.4
425	216	38.0
465	80	42.5
505	17	41.2
545	7	71.5
Weighted per cent	6364	14.6
Standardized per cent		26.6

TABLE 7.—*Incidence of pregnancy*

	NORWAY RATS (OVER 14")				ROOF RATS (OVER 15")			
	1925–7	1926	1928	1925–8	1925–7	1926	1928	1925–8
Total large female rats examined.....	2540	4300	4325	13165	1324	1458	851	3633
Prevalence of pregnancy*	.231	.195	.212	.213	.308	.251	.235	.265
Incidence of pregnancy.....	4.69	3.96	4.30	4.33	6.25	5.10	4.77	5.38
Embryos per large female per year*..	42	36	39	39	45	37	37	40

* All values were standardized to compensate for seasonal differences in numbers of rats examined.

3. The prevalences in Table 7 were obtained by averaging the monthly percentages of Tables 2 and 3 in order to standardize them for monthly changes in prevalences. It will be noted that both species produced about the same number of young each year. Although roof rats had a higher incidence of pregnancy, the number of embryos was smaller. It is likely that 40 young born per year per adult female is a reasonable general conclusion. (Strictly speaking, the data refer to embryos reaching 13th day of pregnancy). It must be noted that mortality occurs at parturition and during weaning so that the number of young weaned is much lower than 40.

SUMMARY

Data on the reproductive condition of a large series of Norway rats (12,962 females) and roof rats (3,633 females) were collected from 1925 to 1928 in San Francisco. The rats were captured in steel traps in commercial areas and autopsied in the laboratory. Prevalence of pregnancy for Norway rats had peaks in May and September, but for roof rats no regular fluctuations were apparent. Norway rats (2,768 pregnant "large" females) averaged 9.0 embryos, and roof rats (978 pregnant "large" females) averaged 7.3 embryos. There were no regular seasonal trends in mean embryos. Norway rats showed some resorption of embryos (6 per cent). Prevalence of pregnancy increased with length or weight of Norway rats, but number of embryos did not. The incidence of pregnancy was 4.3 per "large" Norway rat female and 5.4 per "large" roof rat female, per year. The respective embryo rates per year were 39 and 40.

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ADDITIONAL MAMMALS FROM THE REXROAD FAUNA

By Thomas M. Oelrich

Continued excavation of the several localities in the Upper Pliocene Rexroad formation has not only added to the completeness of the fauna as a whole but has brought forth additional material which adds to the description and the interpretation of the material previously recorded.

The specimens described in this paper were collected in the summer of 1950–51 by the field parties of the University of Michigan Museum of Paleontology under the direction of Dr. Claude W. Hibbard. The specimens are from Meade County, Kansas, localities No. 3 and UM–Kl–47 (Hibbard, 1950).

The author is indebted to Dr. Hibbard for guidance throughout the preparation of this manuscript. Appreciation is extended to Dr. W. H. Burt, Museum of Zoology, University of Michigan, for the loan of recent skeletal material, and to Dr. Robert W. Wilson, Museum of Natural History, University of Kansas, for the loan of the type and paratype of *Procyon rexroadensis*.

Carnivora

Procyonidae

Procyon rexroadensis Hibbard (Hibbard, 1941*a*) has previously been known from the holotype, an isolated left M^1 and a referred right P_4 (Hibbard, 1941*a*). The specimen described here (Fig. 1A, B, C) was found by the author, a member of the field party of the University of Michigan Museum of Paleontology, in the summer of 1950 at locality No. 3, W. ½ SW. ¼ sec. 22, T. 33S., R. 29W., Meade County, Kansas, the type locality of *Procyon rexroadensis*. Comparison with the type specimen indicates that the size of the two specimens was the same and that the occlusal contact of the teeth was readily attainable. Because of this similarity the lower jaw is assigned to the species *P. rexroadensis*.

This specimen is a nearly complete lower left ramus, No. 26997 U.M.M.P., missing only the incisors and the condyle. The mandible is as large as that of *Procyon cancrivorus* (Cuvier).

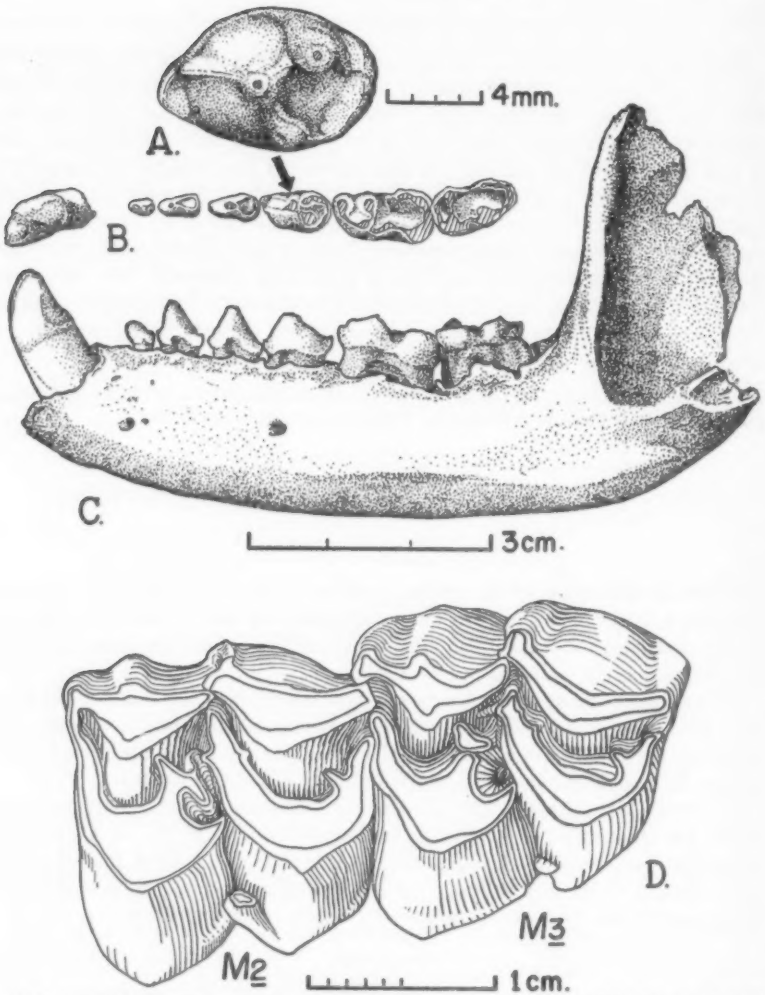

FIG. 1.—A–C, *Procyon rexroadensis* Hibbard: A. Occlusal view of right P^4, Paratype K. U. No. 5523; B. Occlusal view of left ramus U.M.M.P. No. 26997; C. Lateral view of same. Drawings by William L. Bruden. D, *Odocoileus brachyodontus*, new species, occlusal view of left M^2—M^3, Holotype U.M.M.P. No. 28140. Drawing by Jane S. Mengel.

Its ventral border is horizontal and is not convex as in *P. lotor* (Linnaeus) and *P. cancrivorus*. The ventral border extends horizontally further anterior and ascends almost at a right angle to the incisors, while in Recent forms, mentioned above, the inferior border ascends toward the incisors in the shape of an arc (Fig. 1C).

The ascending ramus is almost perpendicular to the occlusal surface of the teeth. It is

distinctive in that it is very thick at its base and tapers only gradually to the coronoid process. This produces a very thick anterior border to the coronoid process and is reflected in the increased depth of the coronoid fossa. In both *P. lotor* and *P. cancrivorus* the base of the ascending ramus becomes thin immediately above the M_2 and forms a very thin anterior border to the coronoid process. The ramus does not decrease in depth toward the anterior and posterior ends as markedly as in *P. lotor* and *P. cancrivorus*. The occlusal surface of the teeth is almost horizontal.

The length of the occlusal surface of the teeth is identical with specimen No. 46407 of *P. cancrivorus*. This is peculiar in that the width of the teeth is much narrower than in *P. cancrivorus* and the dental pattern somewhat less complex than either *P. lotor* or *P. cancrivorus*. The main difference in dental characters of the teeth is the simplicity of P_4 and the narrowness of the premolar and molar series.

P_1 in *P. rexroadensis* is not as greatly reduced proportionally in size as is the P_1 in either *P. lotor* or *P. cancrivorus*. The heel of P_1 is larger than in the two Recent species.

P_2 and P_3 are approximately equal in size and have very similar characters. They both have a small heel which is not as large as that found in *P. lotor* and *P. cancrivorus*.

The P_4 in specimen No. 26997 U.M.M.P. is worn. Determination of cusps is therefore difficult. There is however the paratype, a right P_4, No. 5523 University of Kansas Natural History Museum, which is unworn. The measurements of this P_4 were given by Hibbard (1941*a*) along with the type description. The measurements are as follows. "Referred P_4 has an anteroposterior diameter of 8.8 mm. and the greatest transverse diameter of 6.0 mm." It will be noted by referring to the table of measurements that this P_4 is slightly larger than the specimen described here. See also comparison of occlusal surfaces in Figure 1A, B.

P_4 is distinct in that the cusps are not as well developed as in Recent species. There is a small heel that is constricted anteroposteriorly and does not have a basin. It may be described as a cingulum. It is much like that found on the P_2 and P_3. The protoconid and the hypoconid are well developed and proportionally the same as those found in *P. lotor*. The metaconid is small. It is actually only a projection on the posteromedial surface of the protoconid. In *P. lotor* the metaconid is almost as large as the hypoconid. The bases of these two cones are sufficiently large to cover the posterior slope of the protoconid and separate the base of the protoconid from the heel. In *P. cancrivorus* the metaconid is larger than the hypoconid. Due to the smallness of the metaconid in *P. rexroadensis* the base of the protoconid is not separated from the heel by the bases of the metaconid and the hypoconid. The posterior surface of the base of the protoconid forms the anterior border of the heel (Fig. 1A).

The premolar series in *P. rexroadensis* seems to represent a generalized condition because the P_1-P_3 are not as reduced in size as in the Recent forms and because the cusps of P_4 are not as well developed.

The molar series is proportionally narrower and not as massive as that of *P. cancrivorus* but the molar series resembles *P. lotor* in some respects. The differentiation of a talonid and trigonid in *P. rexroadensis* is much more pronounced than in either of the Recent forms. The trigonid is elevated slightly above the talonid while in the Recent forms they are nearly equal in height.

The cusp pattern of M_1 is identical with that of the Recent forms, but the cusps are not separated by external grooves nor is there any elaborate folding of enamel of the teeth as in Recent forms. The basin of the trigonid is open as in *P. lotor* and not closed as in *P. cancrivorus*. The entoconid is not as well developed as in Recent forms and it does not join the base of the metaconid to close off the basin of the talonid. There is the beginning of an accessory conulid just anterior to the entoconid.

M_2 is the size of the M_2 in *P. lotor*. The cusps are simple. The hypoconulid is not as well developed nor as posteriorly isolated as in *P. lotor*. The lingual valley between the metaconid and entoconid is almost as wide as in *P. cancrivorus*, and there is no entostylid as in *P. lotor*.

Discussion.—Procyon rexroadensis is the oldest known *Procyon*. There are several pro-

cyonids known from the Pleistocene. Two of these are *Procyon simus* Gidley, from California, and *P. nanus* Simpson, from Florida. *P. rexroadensis* resembles *P. simus* in general shape and in massiveness of jaw, but the latter is smaller in size, and the tooth characters of *P. simus* are indeterminate from Gidley's account. *P. nanus* Simpson, from Florida, is known from a maxillary and is smaller than the Recent *P. lotor*.

Procyon priscus Le Conte, from Illinois, and *P. psora* Gray, from California, have been described from late Pleistocene and Recent specimens and are probably referable to *P. lotor*.

P. rexroadensis resembles *P. lotor* in tooth pattern and is not as highly specialized as *P. cancrivorus*. The outstanding characters of this specimen are those which seem to indicate a more generalized condition than shown in any of the known fossil or Recent forms. These are the somewhat unreduced premolar series, the smallness of the metaconid on P_4, the separation of the trigonid and talonid, the simple cones without folded enamel, the massive rectangular jaw, the deep coronoid fossa, and the thick anterior coronoid ridge.

TABLE 1.—*Measurements of Procyon rexroadensis U.M.M.P. No. 26997, in millimeters*

Length of jaw (greatest length)			89.0 mm.
Depth of jaw (between M_1 and P_4)			17.5 mm.
Thickness of jaw (midpoint below M_1)			8.2 mm.
Length of occlusal surface P_1–M_3			48.0 mm.
Width at base of coronoid process			10.0 mm.
P_1, greatest length	3.5 mm.	P_4, greatest width	5.4 mm.
P_1, greatest width	2.5 mm.	M_1, greatest length	12.0 mm.
P_2, greatest length	5.8 mm.	M_1, width of trigonid	6.7 mm.
P_2, greatest width	3.6 mm.	M_1, width of talonid	7.5 mm.
P_3, greatest length	6.4 mm.	M_2, greatest length	10.6 mm.
P_3, greatest width	4.0 mm.	M_2, width of trigonid	6.4 mm.
P_4, greatest length	8.3 mm.	M_2, width of talonid	6.2 mm.

EDENTATA

MEGALONCHIDAE?

Megalonyx? sp. An isolated maxillary tooth, No. 26999 U.M.M.P., was recovered from Meade County locality No. 3. The tooth is rectangular and slightly rounded on its anterior margins. The base of the tooth is broken preventing a determination of the length. The width of the tooth is 21.0 mm. and its anteroposterior length is 12.0 mm. The tooth is not as wide and not triangular as the last superior molar of *Megalonyx leptostomus* Cope from the Blanco beds of Texas.

Other fragments of *Megalonyx*? have been recorded from the Rexroad formation (Hibbard and Riggs, 1949: 835, Pl. 5, Fig. 7). The specimen is referred questionably to the genus *Megalonyx* until better material is known from this locality.

ARTIODACTYLA

CERVIDAE

Odocoileus brachyodontus, new species

Holotype.—No. 28140, University of Michigan, Museum of Paleontology, consists of an associated left M^2 and M^3 of a young adult showing only moderate wear. Paratype No. 28139 U.M.M.P. consists of two left M^3 in more advanced stages of wear.

Horizon and type locality.—Upper Pliocene, Rexroad formation, sec. 35, T.34S, R.30W., Fox Canyon, XI Ranch, Locality UM-K1-47, Meade County, Kansas.

Diagnosis.—A deer having a brachyodont, low-crowned tooth with the dentine of the anterointernal and the posterointernal crescents separated to the base of the tooth.

Description of Holotype.—The teeth (Fig. 1D) are almost identical in pattern with the Recent *Odocoileus* group and slightly larger in size. The M^2 is 15.0 mm. long and 18.0 mm. wide indicating that the tooth is wider than long. This greater width is caused by the massiveness of the anterointernal and posterointernal crests of both M^2 and M^3. The dentine in the protocone and the metaconule is of greater width than in Recent forms. In Recent *Odocoileus* the M^2 and M^3 are as wide as long. The crown is 8.0 mm. high on the lingual side and 11.0 mm. high on the labial side. This is very low when compared with a specimen of *Odocoileus virginianus* Rafinesque at the same stage of wear. In *O. virginianus* No. 61010 U.M.M.Z., the crown measures 10.0 mm. on the lingual side and 12.0 mm. on the labial side. The parastyle of *O. brachyodontus* is poorly developed and the mesostyle extends at right angles to the tooth.

The M^3 is 17.0 mm. long and 19.0 mm. wide. The crown is 10.0 mm. high lingually and 12.0 mm. high labially. The parastyle is more prominent on the M^3 than on the M^2. There is a protostyle on both M^2 and M^3 and evidence of a cingulum on the anterointernal and posterointernal crescents of both the M^2 and M^3.

On the posterior border of the anterointernal crescent of both the M^2 and the M^3 is a loop or fold which remains open nearly to the base of the tooth. In later stages of wear of the M^3 the loop is closed off to form a fossette at a crown height of 4.0 mm. In Recent specimens of *Odocoileus virginianus* this fold forms a fossette in young adults and is almost completely worn away when the crown is 3.0 mm. high.

The dentine of the anterointernal and posterointernal crests in *O. brachyodontus* does not become confluent at the base of the tooth in advanced stages of wear. The enamel of these two crests approximate each other closely and may fuse at the base of the tooth.

Discussion.—Hibbard (1941*b*) recorded a cervid from Meade County, Kansas locality No. 2A and 3. The specimen from locality No. 2A was the tip of an antler.

Procoileus edensis Frick (1937) is the only cervid which has been named from the Upper Pliocene. It is known only from horns and lower rami. *Odocoileus brachyodontus* is distinguished from *Procoileus edensis* by lower crowned teeth, based on a comparison with a series of Recent specimens of *O. virginianus* with comparable stages of wear.

There are several species of Pleistocene *Odocoileus* which have been described from antlers and lower dentitions that possess higher tooth crowns, as in Recent species. *Odocoileus cascensis* Frick is known from a complete right maxillary that has a much simpler pattern than the specimen described here.

Merriam (1915) recorded a "*Cervus* or *Odocoileus*" from the Upper Etchegoin area, North Colings region of California. The specimens are fragmentary antlers and come from deposits which Merriam considered as late Pliocene.

ANTILOCAPRIDAE

This family is represented by a complete lower-right, worn dentition P_2-M_3, No. 28138 U.M.M.P., from Meade County, locality UM-K1-47. There is also a nearly complete upper dentition and some isolated upper and lower promolars and molars, No. 26382 U.M.M.P., from Meade County, locality No. 3. *Capromeryx*? has been recorded previously from Meade County, locality No. 2A (Hibbard 1937, 1941*b*).

This group of teeth represents a small antilocaprid with a tooth row measurement, P_2-M_3, of 52.0 mm. The antilocaprids have been described principally from horn cores, and specific identification is difficult with the material at hand. There are, however, several characters in the lower teeth which show the generalized nature of this form. The protolophid and the hypolophid do not fuse to form or enclose a fossette in either P_2 or P_3. This, however, is characteristic of a number of Pliocene genera such as *Capromeryx*, *Toxoceros*, and *Plioceros*. The premolars are double rooted and the roots are well separated. The M_3 does not possess a fourth lobe. This, too, seems to be characteristic of most of the Pliocene forms (Skinner, 1942).

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GENERAL NOTES

ZORILLA I. GEOFFROY AND *SPILOGALE* GRAY, GENERIC NAMES FOR AFRICAN AND AMERICAN POLECATS, RESPECTIVELY

Confusion regarding the correct generic name for the African polecat began half a century ago and still persists. The first valid name assigned to the African mustelid is *Zorilla* I. Geoffroy, 1826. Howell, in 1906 (Proc. Biol. Soc. Washington, 19: 46), mistook *Zorilla* I. Geoffroy, then in current use, for a "Zorilla" attributed by careless authors to Oken, 1816, and declared the name not valid. Without even mentioning I. Geoffroy, 1826, Howell elected *Ictonyx* Kaup, 1835, as a substitute. Hershkovitz (Jour. Mamm., 30: 289, 1949) also exposed the non-Linnaean nature of "Zorilla" as well as all other "generic" names cited from Oken, and (*op. cit.*: 295) restored *Zorilla* I. Geoffroy as the earliest valid name for African polecats. Finally, Ellerman and Morrison-Scott (Jour. Mamm., 34: 114, 1953) because of a misunderstanding of the true nature of the genotype of *Zorilla* I. Geoffroy, declared this generic name applicable to American polecats, currently *Spilogale* Gray, 1865.

That there may be no doubt regarding the definition of *Zorilla* I. Geoffroy (Dictionaire Classique d'Histoire Naturelle, Paris, 10: 215, 1826), originally proposed as a subgenus of *Mustela*, a copy of the first description is given in full herewith.

"Les Zorilles, *Zorilla*. Ils ont avec le système dentaire des Putois, des ongles longs, robustes et assez semblables à ceux des Mouffettes, auxquelles ils ressemblent aussi par leur système de coloration. Par suite de cette modification ils ne peuvent plus grimper sur les arbres, comme le font les autres Martes; mais ils peuvent fouir avec beaucoup de facilité et se creusent des terriers, comme les Mouffettes. On n'a encore distingué dans ce sous-genre qu'une seule espece.

"Le Zorille, Buff. T. XIII, pl. 41; *Mustela Zorilla* et *Viverra Zorilla* des auteurs systématiques, a plus d'un pied du bout de museau à l'origine de la queue; celle-ci a huit pouces environ. Il est généralement noir avec plusieur taches blanches sur la tête, et plusieurs lignes longitudinales de même couleur à la partie supérieure du corps. Ces bandes et ces taches ont assez constamment le même disposition, mais leur étendue proportionnelle varie beaucoup. Cette espèce n'habite pas seulement les environs du cap de Bonne-Espérance; mais elle existe aussi au Sénégal, et sur les bords de la Gambie, ou elle a été trouvée par le malheureux voyageur Bodwich. Le Zorille du Sénégal et de la Gambie diffère d'ailleurs de celui du Cap à quelques égards: ainsi on retrouve bien chez l'un et chez l'autre les même taches et les mêmes lignes; mais chez le premier, les parties blanches ont beaucoup plus d'etendue que les noires, en sorte que le pelage est presque entierement blanc sur le dessus et les côtés du corps, tandis que la disposition inverse s'observe dans la variété du Cap. Nous ne pensons pas neanmoins qu'on doive considérer ces deux Animaux comme des espèces distinctes: car l'étendue proportionnelle des taches blanches varie même tellement entre les individus d'un même pays, qu'il est assez difficule d'en trouver deux exactement semblables."

Apart from an equivocal bibliographic reference in the designation of the genotype, a matter dealt with below, nothing in the description of *Zorilla* refers to anything else but African polecats. The name *Zorilla* cannot be used for American polecats, genus *Spilogale*.

GENOTYPE OF *ZORILLA* I. GEOFFROY, *MUSTELA ZORILLA* E. GEOFFROY

Zorilla I. Geoffroy is monotypic in the original description and its type is designated as (*supra cit.*) "Le Zorille, Buff., T. xiii, pl. 41; *Mustela Zorilla* et *Viverra zorilla* des auteurs systematiques." The designation is composed of three elements. The first is a bibliographic reference to the figure of Buffon's *zorille*. The depicted animal was regarded by I. Geoffroy as an African polecat. This opinion has been challenged. In any case, whatever the true or fancied identity of Buffon's *zorille*, the animals actually described by I. Geoffroy were, and remain, African polecats, then subgenus, now genus, *Zorilla*. The second element of the genotypic designation is *Mustela zorilla*, the specific name actually used by I. Geoffroy for polecats of his subgenus *Zorilla*, genus *Mustela*. *Viverra zorilla*, the third element, appears in the genotypic designation as an equivalent of *Mustela zorilla*.

The name *Mustela zorilla* is traceable to E. Geoffroy who defined it in 1803 (Cat. Mam. Mus. Nat. Hist. Nat., p. 102). The original description is based on a skin (probably mounted) with Paris Museum catalog number 120. A paratype, number 121, was described as differing only slightly from the type. A second paratype, number 122, was said to be preserved in spirits. The type series is from "l'Afrique septentrionale." Besides the characterization of the species and listing of specimens examined, E. Geoffroy included in the synonymy of *Mustela zorilla*, the following citations:

"Blaireau puant, Kolbe Desc. dup Cat. t. 3, p. 86.

"Le Zorille, Buff. Daub. t. 13, p. 289–302, pl. 41.

"Viverra zorilla, Schreb., tab. 123.

"————Lin. Gml. p. 88."

The *blaireau puant* is the French version of Kolbe's Cape *Stinkbingsem*, and certainly a representative of *Zorilla*. Status of Buffon's *zorille*, with name *Viverra zorilla* Schreber, and Gmelin, based on it, is controversial. Should Buffon's *zorille* prove to be quite distinct from the African polecat E. Geoffroy believed it to be, the type specimen for the name *Mustela zorilla* was and remains the north African polecat, number 120 of the first catalog of specimens of mammals in the collection of the Paris Museum.

A more detailed description of what could only be the type specimen of E. Geoffroy's *Mustela zorilla* was given by Desmarest in 1818 (Nouv. Dict. Hist. Nat., 19: 379) and another by Cuvier, together with a figure of the "Zorille du Cap," in 1823 (Dict. Sci. Nat., Paris, 29: 254, text, and vol. Planches, Zool. Mamm., pl. 34, fig. 1). In the same work (59: 499, 1829) Cuvier formally gave generic rank to *Zorilla* I. Geoffroy, with type, the only known species "qui est du Cap."

The South African locality given by Cuvier for the genus applies only to Buffon's *zorille*

identified by Cuvier as the Cape polecat. The type locality of E. Geoffroy's *Mustela zorilla* is "l'Afrique septentrionale." This should be restricted to the Gambia River, the North African locality mentioned by I. Geoffroy in his description of polecats in the Paris Museum. *Mustela zorilla senegalensis* J. B. Fischer, (Syn. Mamm., p. 218, 1829), based primarily on the Bodwich specimen from the Gambia, is a synonym. This arrangement does not disturb current classification of south African polecats.

The name *Mustela zorilla* E. Geoffroy, as representative of North African polecats, is perfectly valid and available. It is not a synonym of *Viverra mapurita* Müller, 1776, *Viverra zorilla* Schreber, 1777, and *Viverra zorilla* Erxleben, 1777, all based on one or more species of American mustelids plus Buffon's *zorille*. The latter, if an African polecat, is restricted to the Cape form. Lacépède's identically named *Mustela zorilla* is based only on Buffon's *zorille*. The homonym appears in volume 14 of the Didot edition of Buffon's Histoire Naturelle, p. 163, with publication date on title page "An VII" which is 1799. However, the volume was not published before October 1802, and was not issued until late in 1803 (See Sherborn, Nat. Sci., 15: 406, 1899, and Richmond, Auk, 16: 326, 1899). Geoffroy's Catalogue was issued the same year but priority, by choice of even date, is given to *Mustela zorilla* E. Geoffroy.

STATUS OF BUFFON'S ZORILLE

Buffon's erratic description of the *zorille* (Histoire Naturelle, 13: 289, 295–298, 302-3, pl. 41, 1765) is non-Linnaean and non-technical. It would have no taxonomic importance but for the fact that several Linnaean names are rooted in it. Buffon introduces the name *zorille* on page 289 (*op. cit.*) as that of a specimen of polecat loaned to him for description by the parish priest of Saint Louis, Paris. On page 293 Buffon states that the *zorille* and the *chinche* (a *Conepatus*), of which the former may be only a variety, are from South America. On page 295, the *zorille* is compared (in footnote) with the Mexican *zorilla* (*Mephitis* or *Conepatus*) and, continuing on page 296, is said to be the same as the Orinocan *mapurita* (a *Conepatus*). On pages 287–298, Buffon supposes that Kolbe's African mustelid is really an American polecat. There is no implication that Buffon identifies the Cape animal with his *zorille*. Finally, pages 302–3, Buffon describes the animal figured in plate 41.

The stripe pattern as described by Buffon on pages 302–303 and figured in plate 41, is diagnostic of *Spilogale*. The white-edged ears, shown convincingly enough in plate 41 and in the photographic reproduction of the same plate presented by Ellerman and Morrison-Scott (Jour. Mamm., 34, pl. 1, 1953), are diagnostic of the African polecat. All other characters given in the text and visible in the figure are common to African and American polecats. Hershkovitz (Proc. Biol. Soc. Washington, 62: 13, 1949) determined the *zorille* as African because of its white-edged ears. Ellerman and Morrison-Scott (*supra. cit.*, p. 114) insisted on the stripe pattern as critical in identifying the *zorille* as North American. In this case neither criterion is conclusive, and insistence upon that of stripe pattern alone entails an unhappy train of consequences. The polecat of Catesby (A Natural History of Carolina . . ., vol. 2, p. 62, pl. 62, 1754) which is sole basis for the Linnaean *Spilogale putorius*, has stripe pattern of back like that of African polecats. Its ears, however, are entirely black. Buffon gives a copy of Catesby's figure of the polecat in plate 40 under name *Conepate* (not the *conepatl* of Hernández). The original description of the stripe pattern of back of *Ictonyx* Kaup, current representative of African polecats, agrees with that of *Spilogale*. On the other hand, the white nape mentioned by Kaup is a character not present in any *Spilogale*. Nothing is said of color of ears of *Ictonyx*.

The part of Buffon's description with figure analyzed in the preceding paragraph serves as the only coherent one for attempts to compare and identify the *zorille*. Unfortunately, early Linnaean authors who named the animal did not restrict their descriptions to that of Buffon's on pages 302–303, and figure. Their descriptions, like Buffon's over-all one, are composites. This provides enormous latitude for subsequent identifications, and for interpretations of any citation of, or technical names based wholly or partially on, the *zorille*. To further aggravate the situation, the same criteria for specific determinations that are

decisive when applied to specimens, either cancel themselves out, or are rendered inoperative, when applied to original descriptions and figures such as those of Buffon's *zorille* and Catesby's *polecat*. In the case of such ambiguities, it has been usual to abide by almost any reasonable and feasible proposal of the first reviser. The first authority to establish the fact, or create the illusion, that Buffon's *zorille* is South African, is Cuvier (in Azara, Essais hist. nat. Quad. Paraguay, 1: 239, footnote *a*, 1801, and other subsequent publications including Reg. Anim., 1: 149, 1817). The erasure of Buffon's *zorille* from the faunal list of South America is correct and its representation as a South African polecat was accepted by French mammalogists of the time.

The first author to object to Cuvier's decision was Lichtenstein. In his monograph of the genus *Mephitis*, Lichtenstein (Abh. K. Akad. Wiss. Berlin, 1836: 281, 1838) identified the *zorille* as an American spotted skunk. Howell, in revising the spotted skunks (N. A. Fauna no. 26, p. 12, 1906), may not have disowned Buffon's *zorille*, but he did not adopt it as a member of the genus *Spilogale*. Hershkovitz unconditionally rejected the *zorille* as a *Spilogale* and assigned it to the African genus *Zorilla*. Ellerman and Morrison-Scott, in their haste to return it to the New World, cast out the generic name *Zorilla* along with the *zorille*.

The controversy has now become sterile. It is the writer's opinion that the only remaining solution is to regard Buffon's *zorille* as not certainly identifiable. Hence, all names based primarily on, or subsequently restricted to, Buffon's *zorille* are not available for either American or African polecats. *Viverra mapurita* Müller (not *mapurito*) proposed by Hershkovitz (*op. cit.*) for African polecats, is replaced by *Mustela zorilla* E. Geoffroy. The synonymy of genera and genotypes of the African polecats in question, will, therefore, include the following.

ZORILLA I. GEOFFROY

Zorilla I. Geoffroy, Dict. Class. Hist., Nat., 10: 215, 1826. Genotype, *Mustela zorilla* I. Geoffroy = *Mustela zorilla* E. Geoffroy. Trouessart, Cat. Mamm., 2:258, 1897.

Ictonyx Kaup, Das Thierreich, 1: 352, 1835. Genotype, *Ictonyx capensis* Kaup = *Zorilla zorilla capensis* Kaup [*striatus* Perry?].

Rhabdogale Wiegmann, Arch. Naturg. Jahrg. 4, 1: 287, footnote 9, 1838. Genotype, "Die Zorillen Africa's." Wagner, Schreber's Saugthiere, Suppl., 2: 217, 1841, with monotype *Rh. mustelina* Wagner = *Zorilla zorilla capensis* [*striatus* Perry?].

Zorilla Palmer, Index Gen. Mamm., N. A. Fauna, no. 23, p. 716, 1904. Genotype, "*Viverra zorilla* Erxleben, from South Africa."

Note that author of *Rhabdogale* is Wiegmann, not Müller as cited in G. M. Allen's Check List of African Mammals (Bull. Mus. Comp. Zool., 133: 179, 1939). *Viverra zorilla* Erxleben indicated by G. M. Allen (*op. cit.*, p. 178) as superceding *Ictonyx capensis*, is a composite of North and South American skunks plus Buffon's *zorille*. Erxleben (Syst. Reg. Anim., Mamm., p. 492, 1777) gives the "*habitat in America australi*." Palmer, quoted above in the synonymy of *Zorilla*, originated both "*Zorilla* Oken," cited by recent authors, and the "South Africa" locality of its alleged genotype. Oken never proposed the technical name *Zorilla*. The one he used is the vernacular *zorille* that refers to anything but true *Spilogale* or *Zorilla*. So far as the writer could trace it, knowledge of *Bradypus striatus* Perry, 1810, currently listed as a Cape polecat, was exclusive property of the late Ned Hollister (see Proc. Biol. Soc. Washington, 28: 84, 1915). If its status as a Cape muishond subspecifically distinct from the northern form is confirmed, it should be known as *Zorilla zorilla striatus*.

The writer apologizes for numerous typographical and orthographical errors in his article on the technical name of the African muishond published by the Biological Society of Washington, and cited above. Because of absence from the country while on a museum expedition in Colombia, he was unable to proof-read copy before publication. It may be added that many of the plates in the cited volume 13 of the first edition of Buffon's Histoire Naturelle (1765, not 1755) in the library of the Chicago Natural History Museum, are misnumbered. Each of the misnumbered plates shows the proper animal facing the appropriate page but neither the volume number in the left corner of the upper margin nor the plate and page

number on the right upper corner conform to the actual volume number and position of the plate in the text. Similar typographical errors in numbering the plates occur in other volumes of the set. There may be more defective sets of the first edition of Buffon's Histoire Naturelle.—PHILIP HERSHKOVITZ, *Chicago Natural History Museum, Chicago 5, Illinois. Received March 26, 1953.*

SOREX VAGRANS FIRST REPORTED FROM SOUTH DAKOTA

In 1949, Professor Martin R. Brittan, South Dakota School of Mines and Technology, sent to the Museum of Natural History two alcoholic shrews from South Dakota. One of these (KU 45217), taken three miles west of Rapid City, Pennington County, by J. R. MacDonald, was identified as *Sorex cinereus haydeni* Baird. The other (KU 45218), taken two and one-half miles north of Fairburn, Custer County, by W. J. Lintz, proves to be of the species *Sorex vagrans*. We have tentatively referred this specimen to *S. v. monticola* Merriam on geographic grounds, although certain cranial measurements taken show the shrew to be much smaller than other shrews of this subspecies recorded by Jackson (North Amer. Fauna 51, 1928). This shrew was somewhat decomposed when preserved; consequently, the sex cannot be determined. The cranium was crushed but the rostrum and mandibles are intact. The specimen is a young adult. Cranial measurements in millimeters are: maxillary tooth-row, 4.8; palatal length, 5.5; least interorbital breadth, 2.5. The interorbital breadth is less than that of any shrew of the *vagrans-obscurus* group which we have examined from Wyoming. Brittan (*in litt.*) reported that the collector found this shrew dead in a field of dry stubble approximately one-quarter mile from ranch houses and 100 yards from a dry creek. To our knowledge, this is the first specimen of *Sorex vagrans* reported from South Dakota.—ROLLIN H. BAKER AND JAMES S. FINDLEY, *Museum of Natural History, University of Kansas, Lawrence, Kansas. Received June 13, 1952.*

MICROSOREX, SOREX PALUSTRIS, AND *MICROTUS CHROTORRHINUS* FROM MT. KATAHDIN, MAINE

During a short stay at Mt. Katahdin, I found *Microsorex hoyi* (Baird) as a resident of the high mountain-plateau north of Baxter Peak at an altitude of about 4500 feet. The pigmy shrew inhabited the moss mats under the low, creeping, spruce bushes near the upper margin of the high mountain, dwarf woods. The habitat was entirely dry except for the moisture conserved by the thick moss cover.

A colony of specimens of *Sorex palustris albibarbis* (Cope), of different age and sex, inhabited the northern and northwestern shore of Chimney Pond, situated in the Great Basin at nearly 3000 feet. They were living under big rocks piled up between the foot of the densely wooded slopes of the surrounding hills and the lake shore.

Microtus chrotorrhinus (Miller) were taken in the same place with *Sorex palustris.*—GERD H. HEINRICH, *Dryden, Maine. Received July 29, 1952.*

A FLORIDA SPECIMEN OF LE CONTE'S LUMP-NOSED BAT

Le Conte's lump-nosed bat, *Corynorhinus macrotis* (Le Conte), apparently is uncommon in Florida. Hamilton (THE MAMMALS OF THE EASTERN UNITED STATES: 104, 1943) mapped the range of this species as covering the entire state, but, as far as I am aware, only few actual Florida records have previously been published. Allen (Bul. U. S. Nat. Mus., 43: 58, 1893) listed one specimen from Micanopy, Alachua County, and Sherman (Proc. Fla. Acad. Sci., 7: 201, 1945) mentioned another from Florida Caverns State Park, Jackson County. Moore (Quart. Jour. Fla. Acad. Sci., 2: 50, 1949) reported the species in Orange and Putnam counties. It is therefore of interest to record another example, taken at Silver Springs, Marion County.

This specimen was collected by Mr. John Roess on June 30, 1952. It was clinging to the wall of a limestone grotto during daylight hours. The grotto is an artificial one, built for ornamental purposes; but, overgrown as it is with ferns and mosses, it closely resembles natural limestone caverns which are numerous in the general area.

The bat was an adult male. In life, the dorsal hairs were dark, grayish-black with light, horn-colored tips. These light tips were very inconspicuous, however, and to casual inspection the upper surfaces were grayish-black. The ventral hairs were dark gray with whitish tips which were more evident posteriorly. The hairs of the extreme lower abdomen were cottony white, forming a conspicuous light patch about the genitalia.

The specimen is preserved in the joint collection of Mr. E. Ross Allen and the author.—Wilfred T. Neill, *Research Division, Ross Allen Reptile Institute, Silver Springs, Florida. Received August 8, 1952.*

THE CUBAN FREE-TAILED BAT, *MORMOPTERUS MINUTUS* MILLER

Since the description of the small Cuban free-tailed bat (*Mormopterus minutus* Miller) in 1899 there appears to have been no published record to further specimens nor additional data on its characters and habits. We are indebted to Dr. B. E. Dahlgren, Curator Emeritus, Department of Botany, Chicago Natural History Museum for the gift of 33 specimens, collected in March, 1952, at Omaja, Oriente, Cuba. A palm, *Copernicia vespertilionum*, known to the natives as the "jata de los murcielagos," was cut down and thousands of these bats were found in the mass of dead fronds hanging below the crown of the tree, some of which Dr. Dahlgren was able to capture before they escaped. In another palm of the same species was found a colony of *Artibeus jamaicensis parvipes*.

Some years ago this Museum received two specimens of *M. minutus* by exchange with the Museum of Comparative Zoology, collected by Dr. William J. Clench a few miles south of Guaro, near Preston, Cuba in 1928. An inquiry there brought the following notes from Dr. Clench. "A very large colony of bats lived in a rather tall palm, my guess would be about 2000. This was a live palm, though something had altered its usual growth, causing it to develop 3 to 4 times the number of fronds. The fronds were close-set, maybe an inch or two between the blades. The bats were living well down in the fronds. The guano was one to two feet deep and my guide stated that much of it had been taken by the local farmers for fertilizer. As I recall the area, it was rather open savannah country with scattered clumps of scrub and palmettos." Dr. Allen appears never to have published a note on them.

The series of *Mormopterus* from Omaja contains 16 males and 17 females. They fit closely the very detailed description except in some measurements of the skull, which differences could be due to the method used. As is common in other members of the genus, the males have a large gular sac at the lower edge of the throat.

The measurements are: forearm, male 29.0–31.0 mm.; female 28.7–30.8 mm. One male and one female: forearm 31, 30.8; tail 27.7, 27.4; tibia 9.9, 9.6; ear from meatus 10.1, 9.7; third finger metacarpal 31.5, 30.9; first phalanx 12.5, 11.5; second phalanx 11.0, 10.1; fourth finger metacarpal 30.5, 30.0; first phalanx 10.2, 10.5; second phalanx 6.6, 7.1; fifth finger metacarpal 20.9, 20.5; first phalanx 8.8, 9.7; second phalanx 3.5, 3.0.

Skull: greatest length 13.8, 13.5; condylo-basal length 13.0, 12.5; palatal length 4.8, 4.8; greatest rostral width 5.8, 5.5; interorbital width 3.3, 3.2; zygomatic width—, 7.9; mastoid width 7.7, 7.5; width of brain case 6.7, 6.5; upper tooth row 5.0, 4.9; width across outside base of canines 3.5, 3.4; outside width across molars 5.6, 5.7.

The synonymy of the species is:

Mormopterus minutus Miller

Nyctinomus brasiliensis Chapman, 1892, Bul. Amer. Mus. Nat. Hist., 4: 316 (part).

Nyctinomus minutus Miller, 1899, Bul. Amer. Mus. Nat. Hist., 12: 173, Oct. 20, 1899. Miller and Rehn, 1901, Proc. Boston Soc. Nat. Hist., 30: 273.

M[ormopterus] minutus Miller, 1907, Fam. Gen. Bats, p. 254.

Mormopterus minutus Miller, 1911, U. S. Nat. Mus. Bul. 79, p. 70. Allen, 1911, Bul. Mus. Comp. Zool., 54: 246.

Type locality.—Trinidad, Cuba.

Type in the American Museum of Natural History, No. 4915. Adult male in alcohol, skull cleaned. Collected March 8, 1892, by Frank M. Chapman. Orig. No. 359.—Colin Campbell Sanborn, *Chicago Natural History Museum, Chicago 5, Illinois. Received August 1, 1952.*

SUPPOSED OCCURRENCE OF THE SHEATH-TAILED BAT IN THE MARSHALL ISLANDS

The sheath-tailed bat (*Emballonura*) was reported from Jaluit Island, Marshall Islands, in 1947 (Sanborn, Fieldiana, Zool., 31: 59–61). As it was the first record of this bat from the Marshalls, and as bats had never been reported from there before, the locality was questioned. The specimens were labeled as collected by G. Yoshino in May, 1933, and were received from Dr. Mitosi Tokuda in 1937 by the Chicago Natural History Museum.

Recently Dr. Teiso Esaki, Professor of Entomology at Kyushu University, Fukuoka, Japan, has written me in reply to a request for information on the probable origin of these specimens. He states that G. Yoshino was stationed at Korror, Palaus, from 1930 to 1937 as economic entomologist at the Industrial Experiment Station of the Administrative Government of the South Sea Islands. He found, on arrival, zoological collections from the South Sea Islands that he sent to various specialists for identification, but many of the specimens had no data or unreliable data. Yoshino himself never visited the Marshalls. We appreciate Dr. Esaki's help in definitely establishing that these bats are not from the Marshalls.—Colin Campbell Sanborn, *Chicago Natural History Museum, Chicago 5, Illinois. Received September 20, 1952.*

THE SCREECH OWL AS A PREDATOR ON THE BIG BROWN BAT

During recent studies on the conditions necessary for successful hibernation in the big brown bat (*Eptesicus fuscus*) some observations were made on population losses due to predation. The population studied was wintering in a network of tunnels dug into the St. Peter Sandstone forming the cliffs along the Mississippi River in St. Paul, Minnesota. These tunnels, with the ceilings varying from about 15 to 30 feet in height, provide shelter for several hundred big brown bats. Starting in the fall of 1949, a considerable number of inverted skins and wings of big brown bats were observed in certain localized areas of the cave. For the most part these were where some light filtered in from the entrance of the cave. The source of these remains was not determined until the fall of 1950 when a screech owl was observed feeding on a big brown bat. The owl was perched on a narrow ledge about 18 feet from the floor. Several wings and inverted skins of bats were found on the floor under this perch. The owl was observed here several times during the winter and new evidence of predation was found each time. It was not possible to estimate the extent of the depredation since rats, house cats, and skunks worked the cave and removed many of the remains of the bats dropped by the screech owl. No observations were made on the actual capturing of bats. Since big brown bats move fairly regularly throughout the winter the owl had three choices for capturing them: (1) while hanging dormant, (2) while partially awake and moving slowly in the cluster, or (3) while in flight about the cave. It seems probable that most of the bats were taken while hanging from the wall.

The habit of the big brown bats of hanging on the walls in the open near the mouth of the hibernation cave probably makes them more vulnerable to owl predation, during the winter, than the other cave bats in this area.—James R. Beer, *Division of Entomology and Econ. Zoology, University of Minnesota, St. Paul, Minnesota. Received June 9, 1952.*

TWO NEW LOCALITY RECORDS FOR MAMMALS IN MINNESOTA

Clethrionomys gapperi (Vigors). On October 6, 1951 a red-backed mouse (No. 1728 in the collection of the Division of Entomology and Economic Zoology, University of Minnesota) was found dead on a road along the north shore of Swan Lake which is near Nicollet, Nicollet County. This is considerably to the south of the known range of this species in Minnesota. The most southerly record had been from Fort Snelling, Hennepin County. This record would indicate that the red-backed mouse may be expected in any of the hardwood areas of southeastern Minnesota.

Napaeozapus insignus (Miller). An adult male woodland jumping mouse (No. 1726 in the collection of the Division of Entomology and Economic Zoology, University of Minnesota)

was captured June 11, 1951, near Cloverdale, Pine County (Section 21, R19W, T4ON). Previously this mouse had been taken in Cook, Lake, St. Louis, and Carlton counties. Specimens from Cloquet, Carlton County represented Minnesota's most southerly known locality. The present record extends the known range to the southern part of the northern type of forest.—James R. Beer, *Division of Ent. and Econ. Zoology, University of Minnesota, St. Paul, Minnesota. Received June 9, 1952.*

TWINNING IN HOODED CAPUCHIN

Records of twins in the New World primate family Cebidae are sufficiently scarce to warrant mention here of the birth of twin hooded capuchins, *Cebus fatuellus paraguayensis*, on August 5th, 1952, in the Zoological Garden of San Diego. The male parent was obtained as a four-year-old in 1927, and since that time he has sired approximately twenty young. His mate for the first ten years was a large-headed capuchin, *Cebus fatuellus variegatus*, and the two yielded a number of young. When it was possible to provide the hooded capuchin with a female of his own kind, the large-headed female was removed from the enclosure. Subsequently, the pair of hooded capuchins began to produce young annually. In both cases, the females produced but a single young at a time. Two other species of *Cebus* monkeys, *albifrons* and *capucinus*, as well as a true pair of large-headed capuchins, have borne young in the collection and in no instance have multiple births occurred. Other cebids which have bred in San Diego include one species of *Aotus*, two of *Pithecia*, and at least five of *Ateles*, and the total number of young reaches several score, yet the yield in each event, prior to this time, has been a single young.—Ken Stott, Jr., *Zoological Society of San Diego, San Diego, California. Received August 12, 1952.*

SIMPLE METHOD FOR IDENTIFICATION OF LEAST WEASEL

Many thousands of weasel skins are received by the Bounty Claims Section, Pennsylvania Game Commission, in claim for bounty. Three species are represented by these pelts—the New York weasel, *Mustela frenata noveboracensis*, Bonaparte weasel, *Mustela erminea cicognani*, and the least weasel, *Mustela rixosa allegheniensis*. Because the least weasel is comparatively rare, an attempt has been made to identify all skins of this species and to map its range in the state from these records.

Fairly regularly the tail of small pelts of least weasels and Bonaparte weasels would be missing and positive identification became difficult. It was discovered that the fur of the least weasel would fluoresce under ultra-violet light producing a vivid lavender color. The fur of the other two species remained a dull brown under the ultra-violet light. Thus, identification is positively and simply made, immediately. It appears possible that this method could be applied to other species difficult to identify by ordinary means.—Roger M. Latham, *Pennsylvania Game Commission, Harrisburg. Received August 18, 1952.*

THE OCCURRENCE OF THE BLACK-FOOTED FERRET IN NEBRASKA

The black-footed ferret, *Mustela nigripes* (Audubon and Bachman), has long been considered rare throughout much or all of its range. The mammal's status in Nebraska has apparently been in keeping with this general idea. Because of a paucity of records, it has been looked upon as one of Nebraska's rarest mammals and relatively little has been known of its distribution within the state. Myron H. Swenk (Proc. Nebr. Acad. Sci., 8 (3): 61–144, 1908) wrote that "the species is not abundant," and stated (p. 130) without further comment that records of occurrence were from Lincoln, Lancaster County (1); North Platte, Lincoln County (2); Marsland, Dawes County (3); Curtis, Frontier County (4); and Kearney, Buffalo County (5). Parenthetical numbers refer to localities correspondingly numbered on the map, Fig. 1.

In Swenk's unpublished notes, made available to us through the generosity of Mrs. Swenk, are entries which appear to clarify in part the above records of occurrence. In 1914, Lawrence Bruner reported to Swenk that a specimen of the black-footed ferret "was killed

within ¼ of a mile of his home at 2314 South 17th Street, Lincoln, in the early 1890's." Swenk further recorded in his notes that "Bruner has also seen this mammal at Marsland, Dawes County, in the Upper Niobrara River Valley." In 1903, Bruner catalogued the Rees Heaton Collection of mammals at Curtis, Nebraska; Swenk and R. W. Dawson re-examined this collection in 1915 at the Nebraska State Historical Society, at which time Swenk noted that "there were 2 specimens" of *Mustela nigripes* "as there also [had] been on October 29, 1903." Swenk's notes also state that "in answer to the question as to the locality where these two specimens were secured, Mr. Heaton replied on February 19, 1917, that 'the Black-Footed Ferrets were killed about 20 years ago. There are a few of these specimens here yet.' "

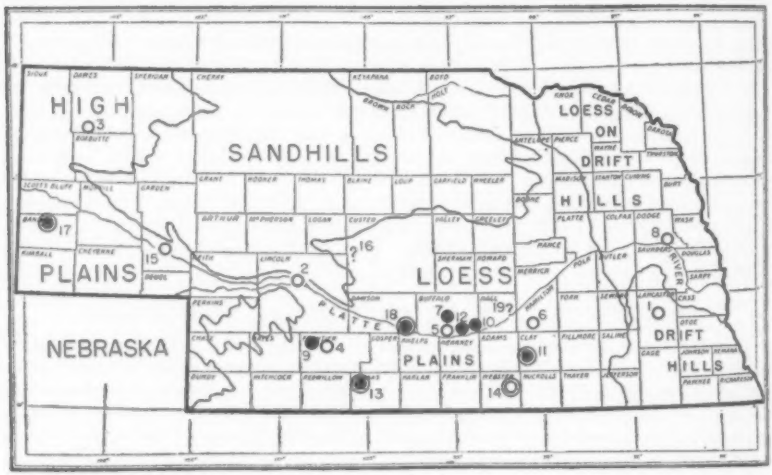

FIG. 1.—Map of Nebraska showing major land types (generalized) and the recorded localities of occurrence of the black-footed ferret. Encircled dots (Nos. 11, 13, 17, and 18): Specimens known to be extant and taken since 1930. Double circle (No. 14): Other record since 1930. Dots (Nos. 7, 9, 10, and 12): Specimens known to be extant and taken before 1930. Circles (Nos. 1, 2, 3, 4, 5, 6, 8, and 15): Other records before 1930. Question marks (Nos. 16 and 19): Localities problematical.

In the introductory remarks of his preliminary review of the mammals of Nebraska, Swenk indicated that a record of occurrence of any species included in his annotated list without discussion of its basis is a "positive record . . . based upon an actual specimen preserved or else upon an observation made by an experienced observer and concerning a common species." The records for Lincoln, Marsland, and Curtis apparently conform to these criteria; the North Platte and Kearney records were presumably admitted by Swenk on the same bases, although clarifying information has not been found.

Swenk's unpublished notes further reveal a report by A. M. Brooking (letters, Brooking to Swenk, April 3 and 20, 1916) that "in the William Townsley Collection there is a specimen of the Black-footed Ferret that was taken by Townsley on his place in Hamilton County, north of Harvard, and that Townsley had known of other specimens being taken in that locality . . ." (6). In August, 1916, Brooking wrote informing Swenk that "in the B. J. Olson collection at Kearney, now in the Kearney Junior High School, is a specimen taken near there that was mounted for Mr. Olson by C. A. Black." A letter from Mr. Paul Morris, Superintendent of the Kearney Public Schools, dated February 3, 1950, reports that the specimen of *M. nigripes* was at that time still in their Olson collection, and that their infor-

mation indicates that the animal was collected in the vicinity of Kearney, Buffalo County (7), by a Mr. O. Blevens. According to Swenk's notes, Brooking was also "authority for the statement that a Black-footed Ferret was killed at Fremont, Dodge County, in the 1920's" (8).

Specimens of *M. nigripes* secured by Brooking for his collection are noted by Swenk, as follows: "In the A. M. Brooking collections [Hastings, Nebraska, Museum] is a specimen (No. 1989) that was killed in a prairie dog town near Maywood, Frontier County (9), on May 12, 1919, by C. J. Pfeifer. A specimen killed about 1927 near Gibbon, Buffalo County (10), by John Shields, is No. 10038 in the Brooking collection. A fine specimen was taken at Glenvil, Clay County (11), January 26, 1938, by Stahnke Brothers . . ." (Hastings Museum No. 18041). These three specimens, plus a second specimen from Gibbon (12), also catalogued under No. 10038, and a skin (No. 19074) collected near Cambridge, Furnas County (13), on April 16, 1939 are now in the collection of the Hastings Museum at Hastings, Nebraska.

In March, 1934, Brooking reported to Swenk that a black-footed ferret had been found dead in the road two miles south of Rosemont, Webster County (14), on March 10, 1934, and brought to Brooking who preserved it as a scientific skin. The disposition of this specimen is not known.

In his notes on the mammals in the collection of Miles Maryott at Oshkosh, Garden County, Nebraska, dated June 14, 1922, Swenk recorded that Maryott reported one specimen of black-footed ferret "that was taken at Oshkosh" (15).

A mounted specimen allegedly from Arnold, Custer County (16), and a skin from northern Banner County (17), are in the collection of the University of Nebraska State Museum, at Lincoln. The latter (UNSM No. ZM3323) was taken by Conservation Officer George Weidman who reported capturing the animal by hand in a prairie dog town nine miles south of Gering, Nebraska, on May 6, 1946. In the collection of the Nebraska Game, Forestation and Parks Commission at its Wildlife Laboratory, Lincoln, is the study skin of a black-footed ferret killed on the road south of Overton, Dawson County (18), on March 16, 1949, and secured by Conservation Officer Burman Guyer. Mr. Ralph Velich of Omaha, Nebraska, reports a specimen of this species in his collection as having been taken near Grand Island (19); the collection date of his specimen is unknown.

The accompanying map graphically summarizes present knowledge of the distribution of *Mustela nigripes* in Nebraska. The preponderance of Nebraskan records in the loess plains suggests a possible correlation between land type and this mammal's habitat requirements. Most, if not all, of the records of occurrence indicate association of the animal with the so-called "hard lands". Twelve of the 19 records variously reported represent specimens taken in areas characterized by loess soils. The black-footed ferret's virtual absence from the sand-hills region of Nebraska, suggested by these data, may be more apparent than real, however; the relatively more thorough coverage of the land by man in the cultivated loess plains, as compared with that of the grazing lands of the sandhills, may have fostered more frequent contact between ferrets and humans and thereby a greater take of specimens. Reasons for the infrequency of records in the loess hills region of east-central Nebraska are not clear.

Many accounts of the black-footed ferret suggest that its distribution is closely correlated with, if not restricted to, the distribution of the prairie dog. It is of interest, therefore, to note here that, in spite of continuing control operations, the prairie dog still occurs, albeit in small, widely scattered colonies, throughout much of Nebraska where no specimens of the ferret have been secured. Prof. O. S. Bare and Mr. Tom Turner have furnished information which indicates current (spring, 1952) or relatively recent "infestations" of prairie dogs in all counties of Nebraska west of the 98th meridian, i.e., throughout virtually all of the state west of the drift and loess-on-drift hills. The rodent occurs in both sandhills and "hard lands". Furthermore, there is nothing in the available data that would suggest a greater abundance of prairie dogs recently in that area of south central Nebraska encompassing most of the later records of occurrence of the ferret in the state.

The distribution of *Mustela nigripes* in Nebraska as indicated by the data presented here

may add significance to the somewhat generalized statement of the mammal's type locality as given by Audubon and Bachman in 1851—"Plains of the Platte River, Nebraska."

For assistance in gathering this information, we are gratefully indebted to the following persons in Nebraska: Prof. O. S. Bare, Entomology Department, University of Nebraska, Lincoln; Mr. W. E. Eigsti, Director, Hastings Museum, Hastings; Mr. Paul Morris, Superintendent of the Public Schools, Kearney; Mrs. M. H. Swenk, Lincoln; Mr. Tom J. Turner, Assistant District Agent, Fish and Wildlife Service, North Platte; and Mr. Ralph Velich, Omaha.—EDSON FICHTER AND J. KNOX JONES, JR., *Department of Zoology, Idaho State College, Pocatello, and Museum of Natural History, University of Kansas, Lawrence.* *Received July 7, 1953.*

ADDITIONAL INFORMATION ON DISTRIBUTION AND VARIATION OF EASTERN BADGERS

Since describing the race of badger, *Taxidea taxus jacksoni* (Schantz, Jour. Mamm., 26: 431, February 12, 1945) the author has examined additional specimens that throw more light on variation and distribution of the subspecies. For the privilege of borrowing specimens in this connection I wish to express my appreciation to Dr. W. H. Burt, Museum of Zoology, University of Michigan; Dr. W. J. Breckenridge, Director, Museum of Natural History, University of Minnesota; Dr. Randolph L. Peterson, Royal Ontario Museum of Zoology, Toronto; Dr. Karl P. Schmidt, Chicago Natural History Museum; Dr. Daniel L. Leedy, U. S. Fish and Wildlife Service; and Dr. Barbara Lawrence, Museum of Comparative Zoology, Harvard University.

The distribution of *T. t. jacksoni* as given in the original description included only the states of Minnesota and Wisconsin. The following records considerably extend the known range of this form.

Michigan: Ann Arbor, Washtenaw County, 3 (1 skin and skull, 1 skin only, 1 skull only, Univ. Michigan); Bow Lake, Charlevoix County, 1 (skin only, Univ. Michigan); Charlevoix County, 1 (skin only, Univ. Michigan); Dexter, Washtenaw County, 1 (skin and skull, Univ. Michigan); Kenton, Houghton County, 1 (skin and skull, Univ. Michigan); Lyndon Township, Washtenaw County, 2 (skins only); Milks Farm, Delta County, 1 (skull only, Univ. Michigan); Munising Township, Alger County, 1 (skin only); Norway, Dickinson County, 1 (skull only, Univ. Michigan); Otter Lake, Lapeer County, 1 (skull only, Univ. Michigan); Patterson Lake, Livingston County, 1 (skull only, Univ. Michigan); Pinckney, Livingston County, 1 (skin and skull, Univ. Michigan); Pittsfield Township, Washtenaw County, 1 (skin and skull, Univ. Michigan); Sands, Marquette County, 1 (skin and skull); Superior Township, Washtenaw County, 2 (1 skin only, 1 skin and skull, Univ. Michigan); Taquahmenaw River, Luce County, 1 (skin and skull); Whitney, Menominee County, 2 (skulls only, Univ. Michigan).

Minnesota: Anoka County, 2 (1 skin and skull, 1 skull only, Univ. Minnesota); Hennepin County, 1 (skin and skull, Univ. Minnesota).

North Dakota: Devils Lake, Ramsey County, 1 (skin only, Univ. Michigan); Grafton, Walsh County, 1 (skin and skull); Lidgerwood, Richland County, 1 (skin and skull); Media, Stutsman County, 1 (skin and skull); Oakes, Dickey County, 1 (skin and skull).

Ohio: Columbus, Franklin County, 1 (skull only); Knox County, 1 (skull only).

Ontario: Port Dover, Norfolk District, 1 (skin only, Royal Ontario Mus. Zool.).

Wisconsin: Mamie Lake, 1 (skull only); Waukesha, Waukesha County, 1 (skull only, Chicago Nat. Hist. Mus.).

The additional material has made possible a more complete knowledge of variation in *jacksoni*, and of the relationship of *jacksoni* to the adjacent races *taxus* and *iowae*. A review of the characters of these forms on the basis of the new material demonstrates that *jacksoni* is a darker race, more reddish buff and more heavily washed with black dorsally, as compared with the silvery-gray or cartridge buff (Ridgway, R., Color Standards and Color Nomenclature, Washington, 1912) and light wash of black and gray of *taxus*, or the light cinnamon drab and light wash of black and gray of *iowae*. *T. t. jacksoni* differs from the dark western

race, *T. t. neglecta*, in its smaller average size. The condylobasal length measurements are indicated by the following: *jacksoni*, 13 males, average 127.2 (119–131.5); 9 females, average 122.5 (117–126.8); *neglecta*, 48 males, 130.9 (123.5–146); 45 females, 124.2 (117.2–131). Another outstanding skull feature is the smaller auditory bullae; these are smaller in *jacksoni* than in *taxus* and *iowae*, and much smaller than in *neglecta*. In the latter they are very prominent. Palatal constriction measurements average greater in *jacksoni* than in *iowae* as indicated by the following: *jacksoni*, ten males, average 15.3 mm. (14–17.3); ten females, 15 (14–15.8); *iowae*, three males, 14.5 (13.6–15.2); one female, 14.

Some evidence of intergradation between *jacksoni* and *taxus* was noted in the North Dakota specimens of *jacksoni*, in that they were slightly lighter in color, and not as heavily washed with black dorsally as the more typical specimens from farther east.

Specimens from Nebraska (Beemer, Columbus, Hastings, Hebron, Johnstown, Pleasanton), South Dakota (Snatch Creek and Fort Randall), and a specimen from 22 miles east of Hill City, Graham County, Kansas, have some of the characteristics of *jacksoni*, but it did not seem advisable to refer them to this race. Also identifying them thusly might imply that this form had a discontinuous range. It may border *iowae* on the east, north and west, but more study of geographic variation is needed on the basis of much more complete specimen material to determine satisfactorily the status of this population.—Viola S. Schantz, *U. S. Fish and Wildlife Service, Washington, D. C.* *Received July 2, 1952.*

RED FOX PREYING ON MUSKRATS

At 6:30 A.M. on June 24, 1952, Gust Gustafson, a farmer who lives on the French River, St. Louis County, Minnesota, (near Duluth), and I saw a red fox coming from the direction of the river carrying something in its mouth. Gustafson shouted and the fox dropped what it was carrying. We recovered the animals the fox had dropped. Two were large and about equal in size. The other three were smaller. One of the large specimens was preserved in formalin and sent to Harvey L. Gunderson of the Minnesota Museum of Natural History for identification. Mr. Gunderson identified the animal as a young muskrat.—Joe Brickner, *763 Armstrong Avenue, St. Paul, Minnesota.* *Received July 28, 1952.*

THE RANGE OF INDIVIDUAL TIMBER WOLVES (*CANIS LUPUS*)

Young and Goldman (The Wolves of North America, Amer. Wildlife Inst.: 74–76, 1944) cite several records of the distances travelled by trapped, tagged, or hunted timber and red wolves. Data on the movements of wolves under natural conditions are sufficiently scarce for the following returns from tagged wolves to warrant recording.

In 1946, the Canadian Wildlife Service initiated a program of ear-tagging and releasing live-trapped coyotes (*Canis latrans lestes* Merriam) and wolves (*Canis lupus occidentalis* Richardson) in the Rocky Mountain National Parks of Western Alberta, under the direction of Dr. I. McT. Cowan, in order to obtain data on the movements of these animals. The recapture of two wolves tagged during this project has yielded interesting information.

The first wolf, a black, female whelp, was dug from a den at the Sulphur Springs on the Panther River, near the eastern boundary of Banff National Park. It was tagged (C. W. S. No. 7) by Cowan and Banfield and released near the den site on July 3, 1946. Clarence Long captured this wolf on his trap line near the Ya-ha-Tinda Ranch on the Red Deer River, sixteen miles east of the den site on April 11, 1950. Both localities are within a well known wolf circuit on the eastern park boundary.

A second dark, male whelp was captured by hand and tagged (C. W. S. No. 809) by Warden Ernest Stenton at the junction of Stony Creek with the Cascade River, in the southeastern section of Banff National Park, on June 13, 1949. This wolf was taken by Warden Frank Camp on November 12, 1951, on the Brazeau River, near the junction of the Southesk River, on the south boundary of Jasper National Park.

The shortest reasonable route from the point of release to the site of capture of this wolf, leads north along the eastern flank of the Rocky Mountains, traversing and crossing seven

main river valleys by way of connecting passes—a distance of 162 miles. The actual route taken by the animal may have been much longer.

It does not seem likely that the entire route lay on the normal circuit of this wolf. More likely the wolf changed its home range sometime after its release.—A. W. F. Banfield, *Canadian Wildlife Service, Banff, Alberta. Received June 12, 1952.*

LONGEVITY OF THE COYOTE

Few figures are available on the life span of the coyote, *Canis latrans* Say. In his lives of game animals (1929, vol. 1: 376), Seton stated that the normal life expectancy should not exceed ten years, but cited the case of one captive female that lived at least fourteen years. In this connection, the recent death of a male, in captivity nearly all his life, seems of general interest. Leo Klever, former keeper, and Earle Harrison, present custodian of the Animal House at this institution, have furnished information on the case. This coyote was one of the subjects in a study of pelage changes, foods, and breeding habits made by Whiteman (Jour. Mamm. 21: 435–438, 1940).

A male and a female, from a litter of five removed from their den on the Hanson Game Refuge, Crawford County, Michigan, came into the possession of this department as pups. Their eyes were still closed and they were probably only a few weeks of age when procured the last week of April, 1937. This pair later raised two litters which were disposed of to other institutions; the female died during the birth of a third litter. In recent years the male has been fed almost entirely on discarded laboratory rats and mice. He has been housed continuously in an outdoor enclosure. He never became docile, but appeared to enjoy good health until early April, 1952. Then there was a gradual loss of appetite and an increasing lethargy. During his last week no solid food was eaten, although much water was taken, and there was a conspicuous loss of body weight, probably totaling several pounds. The coyote lost nearly all motor control toward the end and lacked the strength to resist when he was dispatched with sodium pentobarbitol on April 28, at the age of fifteen years.

His measurements were as follows: total length, 1195 mm.; tail length, 343 mm.; hind foot, 195 mm.; weight, 21 lbs. An autopsy by Roland E. Howell, together with a subsequent pathological examination, revealed an extreme adenocarcinoma of the liver with nearly complete destruction of the hepatic tissue and involvement of the nearby lymph nodes. There was much sanguineous fluid in the thoracic, and considerable in the abdominal, cavities. The malignancy was regarded as a result of senility. In other respects the animal was in good shape. The teeth were complete and not badly worn; the heart and lungs appeared normal; there was no gastric or intestinal obstruction, both organs being empty. The pelage was thick and plentiful except that much hair had been lost from the tail, a condition evident for several years past. The specimen has been deposited in the Museum of Zoology at the University of Michigan, Ann Arbor.—Richard H. Manville, *Michigan State College, East Lansing. Received June 2, 1952.*

RECENT RECORDS OF THE MOUNTAIN LION, *FELIS, CONCOLOR* IN MINNESOTA

Since 1945, we have received more than twenty records of sight observations of mountain lions in Minnesota. Some of these observations could be the result of the lively imagination of the observers, or simply a confusion with the bobcat. Five of the observations, however, were made by individuals whose training in zoology, forestry, and wildlife management, is such that the authenticity of their reports can not be ignored.

On March 7, 1951, Gerald T. Bue examined footprints in the snow near Ghent, Lyon County, Minnesota, which appeared to be those of a mountain lion. Measurements of the prints were taken as follows: width, 4½ to 5 inches; length, 4¼ inches; length of stride, 15 to 17 inches; and the distance laterally from the center line through the left prints to a center line through the right prints, 6 to 7 inches. Plaster casts were made of two of the better imprints. They were sent to Mr. Stanley P. Young of the U. S. Fish and Wildlife Service for identification. In a letter dated April 9, 1951, Mr. Young stated that . . . "there is no question but these casts made of the track are those of a puma. . . ."

On June 8, 1951, John Hale, a biologist of the Minnesota Division of Game and Fish, saw a mountain lion on the Crow Creek Valley Road, Lake County, Minnesota. Later he saw a bobcat on the same road and noted the difference.

Harry Adams, formerly a biologist with the Corps of Engineers, St. Paul, Minnesota, reported seeing a mountain lion along the road a quarter of a mile west of Peter Blackbird's resort north of Cass Lake, Cass County, on September 20, 1950.

On January 22, 1950, three game biologists of the Minnesota Division of Game and Fish, Forrest Lee, John Zorichak, and Gerald Bue, were making an aerial count of deer south of Cascade River, Cook County, Minnesota, when an unfamiliar track was seen. Positive identification was not possible from the air, but the track definitely was not that of a large wolf. Generally, the trail more nearly resembled that of a moose as the foot prints were rather large as compared with the length of the stride. The trail was followed several miles by plane where the animal had traveled along a high ridge, and in one place the animal had crossed a ravine by walking on a fallen tree. It was concluded that the tracks were probably those of a mountain lion.

Finally, Mr. W. Fuller, of the U. S. Forest Service, reported seeing a mountain lion near Two Harbors, Lake County, while hunting grouse in 1948. The lion, crouched on a down tree, was watching a muskrat swim the stream below. It was first detected by the twitching and jerking of the tip of its tail. Two shots fired with light bird shot loads had no noticeable effect on the big cat. Mr. Fuller has had lion experiences in the western states as an employee of the U. S. Forest Service.—Gerald T. Bue and Milton H. Stenlund, *Minnesota Division of Game and Fish, P-R Unit, St. Paul, Minnesota. Received July 15, 1952.*

PHENACOMYS ALBIPES IN LINCOLN COUNTY, OREGON

Two specimens of *Phenacomys albipes* Merriam, collected one mile east of Newport, Lincoln County, Oregon, on June 17, 1942, by Harold E. Broadbooks, were recently discovered in the mammal collection of the Museum of Zoology, University of Michigan. The specimens consist of skins with skulls in excellent condition. The museum numbers and collector's data follow. No. 96042, male, total length, 174 mm.; tail, 71; hind foot, 19; ear, 12. No. 96043, female, total length, 171; tail, 73; hind foot, 18.5; ear, 12. Previously published locality records for this species in Oregon are limited to Vida in Lane County, Blaine and Netarts in Tillamook County, and Gardiner in Douglas County (Walker, Jour. Mamm., 9: 254–255). Since there are few recorded localities and specimens of this species, it seems advisable to make available the information on the two specimens from Lincoln County. For confirming my identification of these specimens I wish to thank Emmet T. Hooper.—W. B. Quay, *Museum of Zoology, University of Michigan, Ann Arbor, Michigan. Received July 1, 1952.*

NICOTINE FACILITATION OF AUDIOGENIC SEIZURES IN LABORATORY MICE

Nicotine-induced convulsions are well known and believed to be due to the stimulating action of nicotine on the central nervous system, mimicking a generalized acetylcholine action (Goodman *et al.*, 1941). Audiogenic seizures in mice look similar to nicotine seizures externally (Frings *et al.*, 1951). This suggests that the same mechanisms may be involved in both types of seizures. As a preliminary test of this hypothesis, a study was made of the possible facilitation of audiogenic seizures by subconvulsive doses of nicotine.

The first experiment was designed to discover the minimum convulsive dose of an aqueous solution of nicotine injected subcutaneously in mice. Three strains of mice were used: *dba*, subline 1; random stock albino; and *C-57* (black), subline 6. While too few animals were used at each concentration to determine lethal dosage accurately, it is interesting to note that the approximate LD_{50}'s for the three strains were: *dba*—5 mg./kg., albino—15 mg./kg., *C-57*—18 mg./kg. These are in the same order as that of susceptibility to audiogenic convulsions, *dba*'s being most susceptible.

On the basis of these results, the dosage levels selected for use with albino mice were 5 and 2.5 mg./kg. The mice were between 20 and 30 days of age, previously untested. Under these conditions, there is a very low incidence of audiogenic seizures (2 per cent) on the first testing day (Frings *et al.*, 1951). In early experiments, each litter was divided into groups

of three mice each, one mouse was treated with sound alone, the second with nicotine alone, and the third with nicotine plus sound. In 28 animals tested with sound alone, only one seizure occurred, thus checking the previous results. Later tests, therefore, omitted the individuals treated with sound alone, and litter mates were treated with nicotine or nicotine plus sound respectively.

The sound-treating equipment and methods have been described in detail previously (Frings *et al.*, 1951). Seizures were induced by irradiating mice imprisoned in a wire mesh cage with sound at 10 kc./sec. frequency and 110 db. average sound pressure. In animals treated with nicotine plus sound, the nicotine was injected subcutaneously, the mice were put into the testing cage, and the sound was turned on 15, 30, or 60 seconds after the injection. Different time intervals were tried to find, if possible, the best.

Of 36 treated with nicotine alone, 4 (or 11 per cent) had convulsions. Of 46 treated with nicotine plus sound, 18 (or 39 per cent) had convulsions. The results with the two groups are significantly different (Chi Square= 6.7). Nicotine definitely facilitates sound-induced seizures in mice. This has been observed also for the rat (Humphrey, 1942). Further, all the seizures of animals treated with nicotine and sound were clonic-tonic convulsions terminating in death. Most of the first seizures of albino mice treated with sound alone—induced usually after more than one day of treatment—are subconvulsions or clonic convulsions not resulting in death. Thus nicotine affects audiogenic seizures both qualitatively and quantitatively.

None of the three times of action of nicotine seemed most suitable for all animals. There is probably a critical state following injection at which almost all animals would have seizures, but this undoubtedly is characteristic for each individual. Further work, therefore, should be based on the use of some physiological indicator of the action of nicotine before sound-treatment, rather than uniform time intervals. Our later attempts to discover this indicator, however, yielded no better results than the use of arbitrary times.

It would seem that nicotine convulsions and audiogenic convulsions may have the same basic mechanism. At least, a generalized acetylcholine involvement in audiogenic seizures is probable. It may be that a seizure results when stimulation by sound has induced the production of unusually large amounts of acetylcholine in the central nervous system. Such an hypothesis accounts for the threshold-like nature of the induction of seizures and for the time relations of sound-induced convulsions (Fuller, 1950). It further explains the increase in susceptibility to audiogenic seizures as a result of intoxication with chlorinated hydrocarbon insecticides (Frings *et al.*, 1950), which have anti-cholinesterase activity.

Since death in nicotine convulsions is known to be due to respiratory failure, these results support the idea (Fuller *et al.*, 1950) that death of mice in audiogenic convulsions is due to anoxia. The short time (ca. 10 sec.) of respiratory arrest in audiogenic convulsions is matched by an equally short time in nicotine convulsions. While the mechanisms of respiratory arrest in the two cases may be dissimilar, it is obvious that anoxia in such a convulsion can result in death, even though the duration is short. Rats may not die in audiogenic convulsions, as mice do, merely because they are larger and thus have a greater oxygen reserve.

Very few drugs are known to facilitate seizures in rats (Finger, 1947), where studies have been more extensive than in mice. Nicotine may therefore be useful both for induction and facilitation studies, since its action mimics the pattern of audiogenic convulsions so closely. From a pharmacological standpoint, also, nicotine has been rather well studied, and thus a wealth of background data on its action is at hand.

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Hubert, Frings, and Alan Kivert, *Dept. of Zoology and Entomology, The Pennsylvania State College, Pennsylvania.* *Received August 23, 1952.*

DISTANCE PERCEPTION IN *MUS MUSCULUS*

The peanut crop in South Georgia is harvested each year during late summer and early fall by plowing up the vines, shaking them, and then stacking them in large stacks about 20 to the acre. The vines on the stacks are then allowed to dry for approximately three weeks or longer depending on weather conditions. During this short period of drying a small assemblage of animals including *Mus musculus*, *Sigmodon hispidus*, *Rattus norvegicus*, *Elaphe guttata*, *Masticophis flagellum*, *Coluber constrictor*, *Sceloporus undulatus*, *Heterodon contortrix*, *Thamnophis sirtalis*, and *Bufo terrestris* adopt these stacks and their ground shelter as their temporary homes. By far the largest number of individuals in this vertebrate population consists of *Mus musculus* and *Elaphe guttata*. When the peanut vines have dried sufficiently to permit threshing, the entire stack, pole, and cleats are lifted from the ground by means of a tractor hydraulic lift and carried to the threshing machine. This procedure leaves the fields bare of most of the former "cover". As each stack is lifted from the ground usually from one to five *Mus musculus* run from under it. The snake inhabitants are usually exposed when the individual stacks are being taken apart preparatory to being threshed.

The observer had noted that on many occasions when only a few stacks were left in a particular field the mice exposed to the sunlight would make a "bee line" for them or nearby machinery. Peanuts are stacked in rows with about 45 feet between each stack, more or less, depending on the type of peanut and the amount of vines present. It appeared that *Mus musculus* could perceive the outline of a peanut stack, truck, or tractor for at least 45 feet in almost all cases, and somewhat farther in others in an experimental test. Twenty-two mice were captured in a manner that did not injure them and placed in a closed cardboard carton. The mice were then transported to another peanut field approximately 200 yards from the point of capture and released with gloved hands, one at a time, in the peanut field that was bare except for one or two choices of available cover. Fifteen of these mice made almost straight lines to safe cover which was at least 45 feet away, and four of them found cover 40 to 45 feet away after random movement of several feet in different directions. The remaining three mice seemed to be satisfied with a few sprigs of grass near the release point. There appeared to be no particular choice of color in determining where a mouse would seek cover, although peanut stacks seemed to hold an edge over grey, red, and blue trucks and tractors.—Milton Hopkins, Jr., *Osierfield, Georgia.* *Received June 3, 1952.*

INCISOR MALOCCLUSION IN A COTTONTAIL RABBIT

A skull of *Sylvilagus floridanus mallurus* (Thomas) from Mt. Carmel, Hamden, Connecticut, recently received by Yale Peabody Museum, presents an interesting example of hypertrophied, non-occluding incisor teeth. According to Al Young of New Haven, Connecticut, who was present at the time the animal was killed and who gave the specimen to the Museum, the rabbit was an old individual but of small size and thin and undernourished appearance. Its advanced age is confirmed by the state of the cheek teeth which are normal and worn nearly to the roots.

The left lower incisor extends nearly three centimeters beyond the end of the jaw, curving upward in front of the nose. Its tip is smoothly rounded but excessively thin anteroposteriorly, and lacks the normal straight chisel edge. Along the medial posterior surface of the tooth there is wear down to within six millimeters of the alveolus, from contact with the outer surface of the upper incisor. The right lower incisor is missing and its alveolus is filled with spongy cartilaginous tissue. The symphysial region of the lower jaw is diseased, the bone rough, pitted, filled with pockets of cartilage, and showing some exostoses, particularly on the right side. The osteomyelitis does not extend to the lingual surface, and there is no trace of fracture. Both pairs of upper incisors are ingrown. The exposed part of the left I^1 forms a semicircle, pointing inward and upward toward the roof of the mouth; its tip is worn obliquely on the outer or anterior surface, instead of across the posterior side, by partial occlusion against the inside edge of the lower incisor. The second left incisor protrudes seven millimeters from the jaw; it is rather irregular in shape, almost thread-like, in the usual position behind I^1. The first right incisor is longer than the left, forming a complete loop, its rounded and unworn tip curving upward and outward beside the maxillary. The second incisor is shorter than the left, protruding only four millimeters into the groove between the two first incisors.

Evidence of the old age of the animal and the peculiar wear on the incisors suggest that injury or disease resulting in malocclusion occurred late in life. The unequal lengths of the upper incisors are clearly due to wear of the left incisor after onset of the deformity. Cause of the osteomyelitis is not evident. Some accident resulting in forcible extraction of the lower incisor might well have led to infection and subsequent deformity of the symphysis so that the left as well as right incisors no longer were able to meet.

Similar malocclusion with resulting hypertrophy and recurving of the incisors has been observed occasionally in rodents (e.g., *Marmota*, Thorpe, Jour. Mamm., 11: 69–70, pl. 5, 1930; Lincoln, Jr., *ibid.*, 19: 107, 1938), but I am unaware of reports of its occurrence in lagomorphs.

The specimen is preserved in the osteology collection of Peabody Museum of Natural History, Catalogue No. 4492.—Joseph T. Gregory, *Peabody Museum, Yale University, New Haven, Connecticut.* *Received August 18, 1952.*

GROWTH RATE OF NAILS ON ADULT POCKET GOPHERS

This study was made to determine the rate of extrusive growth of nails in pocket gophers and to compare the growth of different nails. Because gophers dig extensively, nails of the forefeet are subject to great wear; and the longest, the middle three, might be expected to exhibit faster growth than the outer nails. The nails on the hind toes might not be expected to grow so rapidly as those on the forelegs since they are used less in digging. The data herein are published to indicate the need for further study on (1) the effect of nutritional changes in diet on growth rate of nails and (2) the factors responsible for the differential growth rate between the various nails.

Five adult pocket gophers (*Thomomys bottae navus* Merriam) were housed in cages containing several inches of soil, and were fed rolled oats, laboratory pellets, and, occasionally, green alfalfa, carrots, and potatoes. By use of a dental engine, equipped with a 1/16-inch coarse carborundum-steel disc, a fine transverse notch was made at the base of each nail on the right front and right hind feet. As measurable growth occurred, a second notch was made at the base of the nail, and the interval between the two was measured with a vernier caliper reading to 0.1 mm. Additional notches and measurements were made as needed. All measurements were made by H. E. Bond. Dr. Melvin E. Smith of Davis, California, kindly provided the dental engine, and Dr. Milton A. Miller aided in the preparation of the manuscript.

There is considerable variation in the growth rate of nails on different toes and of different individuals, as indicated in Table 1. The growth rate of most of the nails on female number 10 was measured for a period of 88 days; hence she provides the most reliable data.

All measurements of each of the ten nails on the five gophers were grouped together when

determining the average mean daily growth rate. For example, the mean daily growth rate of the nails on the fourth front toes of the five pocket gophers was determined by grouping the 14 measurements that had been recorded from the five animals over a combined period of 153 days.

TABLE 1.—*Mean growth of nails in millimeters per day and the standard errors* of the means of five adult pocket gophers*

TOE NUMBER		♀10	♀15	♀24	♂34	♂38	AVERAGE
Right front foot	1	0.13 ± .017	—	0.15 ± .007	—	0.15	0.14–.012
	2	0.23 ± .017	0.16 ± .016	0.28 ± .003	0.29	0.19	0.23–.016
	3	0.27 ± .023	0.22	0.25 ± .016	0.19	0.17	0.25–.021
	4	0.21 ± .015	0.20 ± .020	0.30 ± .021	0.20	0.18	0.22–.013
	5	0.15 ± .019	0.16 ± .020	0.14	—	0.07	0.14–.014
Right hind foot	1	0.14 ± .028	—	—	—	0.06	0.13–.027
	2	0.12 ± .013	0.14 ± .053	—	0.11	0.17	0.13–.010
	3	0.13 ± .016	0.13 ± .007	0.180	0.19	0.14	0.14–.011
	4	0.12 ± .003	—	0.180	—	0.09	0.13–.011
	5	0.09 ± .003	—	0.140	—	0.07	0.09–.032
Number of days included in measurements		64 to 88	18	10 to 24	7	16	90 to 153
Number of times each toe was measured		6 to 8	0 to 2	0 to 2	0 to 1	1	8 to 14

* In calculating the standard deviation n-1 was used rather than n because the samples are small.

TABLE 2.—*Mean daily growth of nails in millimeters and the standard errors of the means of female 10 during two growing periods of 44 days each*

TOE NUMBER	RIGHT FRONT FOOT		RIGHT HIND FOOT	
	Period I	Period II	Period I	Period II
1	0.15 ± .017	0.12 ± .033	0.17 ± .042	0.09 ± .007
2	0.24 ± .019	0.21 ± .025	0.12 ± .020	0.10 ± .021
3	0.32 ± .057	0.23 ± .020	0.14 ± .026	0.12 ± .020
4	0.22 ± .022	0.19 ± .008	0.13 ± .011	0.12 ± .023
5	0.16 ± .020	0.12 ± .033	0.10 ± .016	0.07 ± .012

The mean growth of the center nail of the five gophers is 0.25 ± .02 mm. per day, or about 3.6 inches per year. The mean growth of the nails on all three center toes is 0.23 ± .02 mm. per day, or almost twice that of all the remaining fore and hind nails, which is 0.13 ± .00 mm., and the difference is statistically significant ($t = 4.6$).

Why nails on the center three toes of the forefeet, which also are the longest nails, grow about twice the rate of the other nails is not known. The differential growth may be a fossorial adaptation since the three center toes on the forefeet do most of the work when an animal digs. Even though there is no relationship between the nails and teeth of gophers, it is of interest to find that the relatively soft nails have an extrusive or replacement growth that is so much slower than that of the incisors. In another study, Howard and Smith (Jour. Mamm., 33: 485–487) found that each upper incisor of the same subspecies of pocket gopher

averaged a daily extrusive growth of 0.62 mm., and each lower 0.99 mm., the average rate of growth of all incisors (0.81 mm.) being five times the average growth of all nails (0.16 mm.).

When the series of measurements of female number 10 (Table 2) are divided into two growing periods of 44 days, respectively, the extrusive growth rates are not significantly different, but it is of interest to note that the average daily growth of the nails on all toes was consistently less during the second period. With a larger sample it is quite possible that there would be a significant difference between the rates of growth during the two time intervals.

Whether this difference in growth is caused by a nutritional change in diet or some other factor has not been determined. There was no marked loss in body weight of the animal during the second group of measurements.—Walter E. Howard, *Department of Zoology, University of California, Davis.* *Received August 7, 1952.*

ANIMALS TRAPPED IN MOUNTAIN BEAVER (*APLODONTIA RUFA*) RUNWAYS, AND THE MOUNTAIN BEAVER IN CAPTIVITY

The author's current investigations into the reproductive cycle of the mountain beaver (*Aplodontia rufa*) have necessitated extensive trapping since early in 1949. No. 0 and No. 1 steel traps were set, without bait, at strategic locations in the subterranean runways. About five to eight traps per system of runways were generally adequate to secure any beavers present within the first two nights of trapping. Except in the breeding season, usually only one mountain beaver inhabits a runway system.

My trapping has been carried out in the Cascade mountains of southern British Columbia, at the head of the Willamette Valley in Oregon, and at Pt. Reyes and Lake Tahoe in California, and has yielded 75 mountain beavers. In this period a considerable number of species other than *Aplodontia rufa* have been caught inadvertently in the runways of this animal. Thirty-six individuals of 13 other mammalian species, plus one amphibian (*Dicamptodon ensatus*), were also trapped. Members of the Mustelidae were most commonly caught, as nine spotted skunks (*Spilogale putorius*), five weasels, and one mink (*Mustela vison*) were taken. Four of the weasels were bridled weasels (*Mustela frenata*) from Pt. Reyes, and the fifth was the Cascade weasel (*Mustela erminea*) from British Columbia. Most of these mustelids were caught during the breeding season of the mountain beaver. Possibly they were hunting its young, since it is doubtful if any but the mink could kill an adult mountain beaver.

Other mammals caught were: one bushy-tailed woodrat (*Neotoma cinerea*), eight dusky-footed woodrats (*Neotoma fuscipes*), two Douglas squirrels (*Tamiasciurus douglasi*), one jumping mouse (*Zapus princeps*), four brush rabbits (*Sylvilagus bachmani*), one California meadow mouse (*Microtus californicus*), one Cascade meadow mouse (*Microtus richardsoni*), one pocket gopher (*Thomomys bottae*), and one white-footed mouse (*Peromyscus maniculatus*). Since the traps were unbaited, it is assumed that these animals were using the runways as an easy avenue of travel or as hunting grounds.

Several mountain beavers have been maintained for long periods of time (six months or more) in small laboratory cages designed for rabbits and guinea pigs. Adults have gained weight during captivity even after badly damaging themselves in the trap. They have also recovered completely from such operations as ovariectomy and epididymal biopsy. These facts discount some of the statements made in the literature that the mountain beaver is hard to keep in captivity. Lettuce, carrots, apples, and whole-wheat bread keep the animals in good condition. Large amounts of water are also necessary, and it is imperative that individuals be kept in separate cages. Males will kill females as well as each other, and this situation has, as yet, prevented any breeding in captivity.—E. W. Pfeiffer, *Museum of Vertebrate Zoology, University of California, Berkeley.* *Received July 28, 1952.*

A RECORD OF NORTH AMERICA'S MOST WESTERLY MOOSE

A bull moose (*Alces alces gigas*) was killed at Cape Prince of Wales on Alaska's Seward Peninsula on September 20, 1948, by the writer and two Eskimos. This record is considered

noteworthy because Cape Prince of Wales (lat. 65° 36′ N., long. 168° 05′ W.), constitutes the most westward extremity of the North American continent, and is separated from the periphery of normal habitat for moose by nearly two hundred miles of mountains and arctic tundra. Native residents of the area had never before seen a moose, though two of the older reindeer herders mentioned that many years ago they observed a single shed antler from such an animal several miles inland. W. B. Quay in his "Observations on Mammals of the Seward Peninsula, Alaska" (Jour. Mamm., 32: 88–99, 1951) does not mention moose as occurring in that region.

Dr. John L. Buckley of the Cooperative Wildlife Research Unit at the University of Alaska has concluded, on the basis of dentition, that the moose was about twenty-eight months of age. Although in extremely lean condition, the animal showed no abnormalities upon being butchered. The skull of this moose has been deposited in the University of Alaska Museum.—James W. Brooks, *University of Alaska, College, Alaska. Received July 20, 1952.*

UNUSUAL "CURIOSITY" BEHAVIOR ON THE PART OF AN *ODOCOILEUS HEMIONUS* DOE

At about 7:00 P. M. on the evening of August 1, 1952, while camped on the edge of a freshly-mowed haymeadow surrounded by cottonwoods on the Oscar Yoder ranch on Bear Creek, Goshen County, Wyoming, the following was observed by the undersigned and Mr. Morton Green of the South Dakota School of Mines and Technology.

It was early twilight, due to a heavy overcast, when a large doe came out of the woods about 200 yards from where we were camped under a cottonwood. She stood and watched us for three or four minutes, and then advanced about 50 yards into the meadow and sat down on her haunches like a dog, with her fore legs straight and upright. With her head up and her ears cocked forward, she watched us for about five minutes until startled by the sudden movement of a dish towel, at this time she stood up and slowly walked off into the woods.

As the hay had been freshly cut there was no need to change position in order to obtain better observation; at any rate, while sitting in this manner her head remained at about the same height as when standing. The action seemed normal to her and she sat down in exactly the same manner as a dog or rabbit.

The deer in this region apparently are familiar with humans, as Mrs. Yoder had told me the night before that they were constantly foraging in her garden.—J. R. Macdonald, *Museum of Geology, South Dakota School of Mines and Technology, Rapid City. Received August 8, 1952.*

REVIEWS

Hooper, Emmet T. A Systematic Review of the Harvest Mice (Genus *Reithrodontomys*) of Latin America. Miscellaneous Publications, Museum of Zoology, University of Michigan, No. 77, pp. 255, 9 pls., 24 figs. in text, 12 maps, tables. 1952. Paper. Price $4.00.

Since 1841 when harvest mice were made known to science by Audubon and Bachman, a great many kinds have been named and many of these were described only superficially. In 1914 A. H. Howell revised the genus and produced a reasonably workable arrangement for the then-known material. As is often the case, however, subsequently collected material proved that certain of Howell's taxonomic conclusions were untenable. The increased amount of material, especially that from Latin America, tended to obscure further, rather than to clarify, the relationships of the named kinds. Hooper has attempted to reorganize the known specimens from Latin America in the light of modern taxonomic thinking, that is, with regard to the biological mechanisms involved in producing the Recent forms. Further, and to me at least as important, he has offered an explanation of the phylogeny of the genus.

The title is slightly misleading because Hooper fortunately has not restricted his study to the Latin American kinds of harvest mice. Cognizance, based on first-hand information, is taken of the variation and distribution of the more northern kinds, and the reader is not confronted with geographic distributions that seem to terminate at some political boundary!

The arrangement of the report is briefly as follows: Introduction, Materials (3,111 specimens examined), Acknowledgments, Methods, Age Classes, Pelages, Breeding Habits, Topography and Nomenclature of the Molar Teeth, lists of kinds treated, keys, taxonomic accounts, and the interpretive sections.

Those sections preliminary to the keys and taxonomic accounts are models of their kind—brief and well balanced. Although these sections do not, of course, dispose of all the student's pertinent questions, they do summarize what is known of the life history of the harvest mice. Also, Hooper clearly indicates what is not known in certain connections, and in places the gaps in our knowledge are conspicuously wide. One wishes, for example, that the data on molts obtained from dead specimens were supplemented by experimental findings; even direct observational evidence is limited to a few kinds by the paucity and seasonal distribution of available specimens. The intimate relation between evolution and ecology has been explored all too little in mammalogy in general, and a perusal of Hooper's notes on the habitats of the various species leads to the conviction that comparative life history studies of Latin American harvest mice should be a fertile field of investigation.

The nomenclature employed for the topographic features of the molar teeth is a composite of that of Hershkovitz and that of Wood and Wilson. The terminology of Hershkovitz is employed for folds and grooves and is essentially descriptive. The Wood-Wilson nomenclature pertains to cusps and ridges and is based on homologies. The combination of the two make a most usable system and one that is sure to come into wide use. Although some persons probably will object to parts of the terminology, it permits the student to know unmistakably to what Hooper refers. Further, since part of the nomenclature is based on homology, the person studying the dental descriptions constantly has before him some of the more significant characteristics from which the natural systematic groupings are inferred.

Hooper's keys are unusually good and meaningful. He has attempted to employ, where possible, those characters of fundamental importance to the systematics of the harvest mice. Conspicuous artificial characters that are of no importance *per se* are employed in a supplemental fashion. The net result is that the keys yield more than a coincidental resemblance to a natural arrangement. Additionally, characters of an obscure, subjective, or relative nature that are used in the keys (and elsewhere, for that matter) are clearly defined and, where feasible, illustrated. Thus a "relatively longer rostrum" always means longer in proportion to the depth of the cranium. In this connection, Hooper's "depth of cranium" is perhaps an unhappy choice of terms because the measurement includes the depth of the audital bullae. The keys are to species.

The taxonomic accounts include description of the characters of the genus, the subgenera (*Reithrodontomys* and *Aporodon*), species, and subspecies. Too often in the past, revisers of groups have but loosely characterized their larger categories, failed to characterize the species, and have described the subspecies only circuitously by comparative terms. I have found such loose taxonomic methodology most annoying, as has anyone who has attempted to ascertain the known morphological limits of some highly variable species—*Peromyscus leucopus*, for example—without undertaking a major revisionary study himself. The only shortcoming in Hooper's paper in this respect is the omission of a direct delimitation and definition of the species-groups. The careful student will nevertheless be able to discover for himself Hooper's criteria for recognition of the species-groups by combing each page for the scattered pertinent comments.

Under the heading of each species-account there are brief statements of distribution, habitat, comparisons, and relationships. The same organization is followed in the account of each subspecies, and includes, additionally, Remarks and Specimens Examined. Some of the more interesting speculative and interpretive statements in the report are under Remarks. Hooper's taxonomic evaluations, so far as can be judged from his data and my limited experience with the genus, are, I think, handled with commendable restraint. He does not, for example, change the nomenclatural designation of any given kind of harvest mouse without cogent reasons and these reasons are clearly stated, not implied. In all, 19 species comprising 56 subspecies are treated.

The real meat of the paper lies in the theoretical and speculative parts. Many of us are content to terminate our taxonomic publications with the purely nomenclatural matters. Perhaps we fear—and with some reason—the criticism of our colleagues for presuming to tread on the thin ice of speculation. Nonetheless the time has arrived when it is incumbent upon every reviser—indeed, every systematist worthy of the name—to assemble his data and then produce an explanation of it. Even Aristotle was aware that understanding, not data, is the goal of science. There are those who in good faith criticize any theoretical considerations as vainglorious padding. To me intentional and careful theorizing is a worthwhile attempt to extrapolate from the raw data to the basic principle and concept. And it is the basic principle and concept, not raw data, that mark the advance of understanding. Hooper has done philosophically what might have been hoped for and has made some succinct interpretations of his findings. His analysis of the probable evolution of the genus seems credible, but regrettably the fossil record is too scanty to lend much assistance to the reconstruction of the phylogeny of the harvest mice. Lacking adequate paleontological support, the interpretations are to a high degree speculative, but are clearly so labelled. Wisely, I think, Hooper has generally skirted the problem of evolutionary time except where known geological events offer some fairly precise evidence of the time factor.

In analyzing geographic distribution, Hooper makes certain preliminary assumptions and bases the ensuing discussion on those assumptions. Some persons will not grant the validity of the assumptions that the region of origin and dispersal of a group of animals is characterized by (1) the greatest number of species, (2) the greatest number of specialized species, (3) a strong tendency for specialization in comparatively generalized species, and (4) strong differentiation among subspecies. Those persons will not, therefore, accept Hooper's conclusions. Unfortunately Hooper does not examine alternative points of view, but he does provide those who disagree with his initial assumptions with a body of facts with which to arm themselves for a rebuttal. Hooper ascribes to the subgenus *Aporodon* an origin in Central America. The primitive *Aporodon* stock diverged into two groups, one in Guatemala, one in Costa Rica. The first of these, the *mexicanus* species-group, gave rise to *R. gracilis* and *R. dariensis* in the arid lowlands, and *R. mexicanus* and *R. brevirostris* in the humid highlands. The second, the *tenuirostris* species-group, similarly split into two main sub-groups, the first containing *R. microdon* and *R. tenuirostris*, the second containing *R. rodriguezi* and *R. creper*. The subgenus *Reithrodontomys* is supposed to have undergone its differentiation north of the Isthmus of Tehuantepec. The *fulvescens* species-group diverged from the main stem in the arid highlands at an early stage. The remaining *megalotis* species-group differentiated into three principal lineages: (1) *R. humulis*, *R. burti*, and *R. montanus*

all differentiated in the semihumid south-central United States; (2) *R. megalotis* and *R. raviventris*, in the arid southwestern United States and the contiguous Mexican Plateau; and (3) *R. chrysopsis* and *R. sumichrasti*, diverging from each other and the main stem at an early stage, arose in the humid Mexican highlands. *R. pratincola*, a fossil species, is regarded but on slender evidence, as a possible ancestor of the *humulis-burti-montanus* series, and *R. simplicidens*, the second known fossil *Reithrodontomys*, as a possible ancestor of the *megalotis-raviventris* series. Among living species, *humulis* or *montanus* is thought to most closely resemble the primitive reithrodontomine ancestral stock.

Editorially the report is, with certain exceptions, well prepared. Type styles and page layout have been well planned so that various subsections are easily located. The style of writing is easily read and almost never subject to misinterpretation, although in places it seems unnecessarily verbose. Some persons will object to beginning sentences with trivial names, which results in the capitalization of those names. There are relatively few errors in the text for a work of this size. One such is "Compared further with *megalotis*, *burti* has a longer tail (70 to 97 per cent of head and body length compared with 94 to 114 per cent in specimens of *megalotis* from the region, . . ." (p. 41). The maps and other illustrations are of much better than average quality. The maps, incidentally, are arranged so that it is possible to determine at a glance between which subspecies intergradation was detected, but not, for mechanical reasons, the geographic extent of such intergradation. Statistics are employed extensively and are handled with skill and and judgment so that they are an integrated part of the report, and not a cumbersome excrescence little related to the textual material proper. Students of distribution will welcome the appended gazetteer which, in addition to pin-pointing localities where possible, tells what specimens of *Reithrodontomys* were obtained at a given place. There are many discrepancies between the specimens recorded under Specimens Examined and the specimens shown in the gazetteer as having been collected at a specific place. Nor are all the localities mentioned in the text given in the gazetteer (Ciudad Hidalgo, Michoacan, p. 76, for example). In stating localities, Hooper has rounded out the distances to the nearest whole mile and altitudes usually to the nearest 100 feet. He feels that, at least when dealing with Latin American localities as known to mammal collectors, "even this may be pseudo accuracy" (p. 221). An inspection of some of the specimens included in the review discloses that in some cases distances were rounded out somewhat more than to the nearest mile.

It is clear that by no means all of the problems, either taxonomic or distributional, have been solved for the genus *Reithrodontomys* and Hooper has carefully pointed out several promising avenues of investigation. Notwithstanding the criticisms mentioned herein, persons familiar with taxonomic treatments of mammals will recognize that Hooper's review of the Latin American 'reithros' contains a substantial body of information treated with considerable taxonomic skill. The net result is a publication that sets a standard for studies of its sort—and a high standard it is indeed.—Keith R. Kelson, *Museum of Natural History, University of Kansas, Lawrence.*

Cockrum, E. Lendell. Mammals of Kansas. Univ. Kansas Publ., Mus. Nat. Hist., Lawrence, Vol. 7, No. 1. 303 pp., 73 figs. (maps). August 25, 1952.

This work is another very useful addition to the series of state books on mammals that have been appearing in recent years. It is much more than a faunal list, and contains information on the present and past status of Kansas mammals, distribution, life history notes, habitats, synonomy, and economics. External and skull measurements of representative specimens are presented also. Distributional maps give ranges and locality records for all forms present in the state, and for some that have been extirpated.

An introductory section describes Kansas and its faunal divisions. The faunal discussion is broad, and compares various ecological concepts of faunal divisions including Merriam's "Life Zones", the biome, biotic provinces, faunal areas, biotic areas and districts, and distributional areas. This last type of faunal division is chosen by Dr. Cockrum as most useful

for Kansas conditions, and he characterizes the distributional areas for Kansas by particular assemblages of mammals. He recognizes two main distributional areas, the Great Plains and the Central Lowland, each with subdivisions.

An informative discussion of distributional problems and speciation in Kansas is presented in relation to various ecologic factors. Some interesting examples of the effects of temporary climatic changes on Kansas mammals are described.

For some groups, such as lagomorphs and canids, there is a detailed discussion of local bounty systems, past and present. Needless to say, such systems have been no more successful in Kansas than elsewhere. Data on the history of market hunting, capture for stocking, and numbers of fur-bearers taken are given for appropriate species.

Useful keys for identification to species are presented and brief discussions of subspecific differences noted in the accounts. Notes are made of existing taxonomic problems.

Much of the life history and reproductive data are given by reference to works that are summaries of the original literature. It might have been better to refer to the original authors for these important data. Like most state works on mammals, *Mammals of Kansas* points to the great dearth of information in relation to many species, and this, indeed, is perhaps one of the greatest values of such a work as this.—W. ROBERT EADIE.

Durrant, Stephen, D. MAMMALS OF UTAH, TAXONOMY AND DISTRIBUTION. Univ. Kansas Publ., Mus. Nat. Hist., Lawrence, Vol. 6. 549 pp., 91 figs. (maps). Agust 10, 1952.

Utah has apparently been the happy-hunting-ground of the mammalogist if one may judge from the describers' names attached to the many species and subspecies (247) of mammals that occur there. Stephen Durrant's name appears in connection with 32 of them and gives some measure of the intensity with which he has pursued his study of Utah mammals over a period of 18 years. *Mammals of Utah* is a substantial work of scholarly scope, and presents the results of a thorough study of the distribution and speciation of the mammals of the state.

In the body of the work each subspecific form is treated under the following headings: accepted scientific name, vernacular name, synonomy (with type localities), range, description and comments (including measurements and complete descriptions), specimens examined, additional records, and tables of cranial measurements. This section of the book is essentially taxonomic, but when the author comes to the mule deer and elk, some additional notes are given on past history and present-day management problems in Utah.

An introductory section sets forth the history of the study of Utah mammals and gives a description of the topography and climate of the state. A perusal of this section gives one a new respect for the hardiness and adaptability of mammals.

Two final sections of the work discuss faunal areas and physiography and speciation. Dr. Durrant has used the topographic areas of the physiographers, and has characterized them by the species-groups of mammals that occur in them. Neither the life zone concept of Merriam nor the biotic provinces of Dice were deemed adequate to describe the complex distribution of Utah mammals, because of the need for finer categories. Six major faunal areas are described, most of which are divided in provinces. Some of the provinces are in turn divided into subcenters, and one of these into districts.

In the section on physiography and speciation, it is evident that much thought and careful study has been devoted to the formulation of some definite concepts to account for the diversity and present distribution of Utah mammals. When one looks at the check list of Utah mammals, it is easy to see the challenging and fascinating problems that exist. There are, for example, five forms of *Ochotona princeps*, two of *Sylvilagus nuttalli*, three of *S. auduboni*, three of *Tamiasciurus hudsonicus*, three of *Marmota flaviventer*, three of *Citellus leucurus*, five of *Eutamias minimus*, and four of *E. quadrivittatus*, to name only a few. However, it is in relation to the pocket gophers and kangaroo rats that Utah really exhibits diversity. There are 11 forms of *Thomomys talpoides*, 24 forms of *T. bottae*, 15 of *Dipodomys ordi*, and six of *D. microps* (not to mention two of *D. merriami* and one of *deserti*).

In his study of the problems presented by this great diversity of mammal forms, Dr. Durrant has arrived at certain conclusions for which he presents detailed evidence. These conclusions are:

"1.—Pleistocene Lake Bonneville, of great size, and fluctuating level, has importantly affected the distribution and subspeciation of small mammals of both the mainland and the now exposed basin.

"2.—The major mountain ranges of Utah have enabled boreal mammals to extend, or retain, their ranges far southward, and have acted as barriers that have prevented many kinds of mammals of the lowlands from crossing to the opposite side.

"3.—The Colorado River, and its large tributary, the Green River, have markedly influenced the distribution and speciation of mammals, and the influence has been progressively greater down stream to the southern boundary of the state.

"4.—Because of secular changes in each of the three physiographic features mentioned above, populations of mammals which are at the limits of their ecological tolerances, and also at the limits of their geographic ranges, have divided into small, terminal populations, which, under semi-isolation, have rapidly evolved into recognizable subspecies.

"5.—Sewall Wright's theory of random fixation of nonadaptive characters is supported by the kind and amount of morphological variation of the numerous endemic subspecies, especially those that are semi-isolated or that have linear ranges."

Interesting time scales for the evolution of subspecies of mammals are presented, utilizing the evidence of physiographic changes and present distribution. Some forms endemic to the islands of Great Salt Lake are thought to have evolved within the last 2000 years.

It is regrettable that in a technical work of this kind there is no room or place for the many interesting field observations and personal experiences that must have been the lot of the author in 18 years of intermittent life-in-the-saddle on the deserts, plains, and mountains of Utah, in search of the specimens that made this book possible.—W. Robert Eadie

RECENT LITERATURE

(Conducted by David H. Johnson, Claude W. Hibbard, Richard H. Manville, and Henry W. Setzer)

[Reprints of this section may be purchased from the Corresponding Secretary]

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Anonymous. The Bertram Mills Circus. Illus. London News, vol. 219, no. 5880, p. 1083, illus. Dec. 29, 1951. (Chimpanzees, tigers, bears, lions)

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SAVAGE, DONALD E. Report on fossil vertebrates from the Upper Magdalena Valley, Colombia. Science, Lancaster, vol. 114, no. 2955, pp. 186–187. August 17, 1951.

SCHNEIDER, KARL MAX. Zur gewichtsmässigen Jugendentwicklung gefangen gehaltener Wildcaniden nebst einigen zeitlichen Bestimmungen über ihre Fortpflanzung.

12. Skin gland activity and pelage descriptions in moles. W. Robert Eadie, *Cornell University, Ithaca.*

7:30 P.M.

Informal Get-together, Staff Cafeteria

WEDNESDAY, JUNE 17

9:00 A.M.

13. What is the biological significance of the subspecies? William H. Burt, *University of Michigan, Ann Arbor.*
14. Skull variation in meadow mice in Pennsylvania. Dana P. Snyder, *Carnegie Museum, Pittsburgh.*
15. Problems in the taxonomy of New World primates. G. E. Erikson, *Harvard University, Cambridge.*
16. A study of the mammals of Arizona: Part I, The Huachuca Mountains. Donald F. Hoffmeister, *University of Illinois, Urbana.*
17. Phylogenetic implications within the subgenus *Citellus* as indicated by present distributional patterns and ecological tolerances. Stephen D. Durrant and Richard M. Hansen, *University of Utah, Salt Lake City.*

10:30 A.M.

Annual Business Meeting, Election of Officers

2:00 P.M.

18. Zoogeography of bats from islands off the northern coast of South America. Karl F. Koopman, *Queens College, Flushing.*
19. Possible causes of an apparent decline in cave bat populations. Charles E. Mohr, *Audubon Center, Greenwich, Conn.*
20. The nasopalatine apparatus of microtine rodents. W. B. Quay, *University of Michigan, Ann Arbor.*
21. The os clitoridis of some North American Sciuridae. James N. Layne, *Cornell University, Ithaca.*
22. Comparative morphology of the body-skeleton in Recent Canidae. Milton Hildebrand, *University of California, Davis.*
23. A comparative study of the kidneys in young and old hamsters. D. E. Balfour and A. L. Soderwall, *University of Oregon, Eugene.* By title only.
24. Recent activities in bat banding. Charles E. Mohr, *Audubon Center, Greenwich, Conn.*

3:30 P.M.

Wives and visiting ladies were invited to visit the Planetarium.

7:15 P.M.

Annual Dinner, Brass Rail

THURSDAY, JUNE 18

9:00 A.M.

25. Testes morphology in adult *Peromyscus maniculatus* in late winter and spring. Paul S. Eskridge, *Colorado A. and M. College, Fort Collins.*
26. A natural parturition of a porcupine and the first reactions of a porcupette. Albert, R. Shadle, *University of Buffalo, Buffalo.*
27. Developmental patterns in the Arctic ground squirrel, *Citellus parryi barrowensis.* William B. Mayer, *University of Southern California, Los Angeles.*
28. Reproduction in the bobcat, *Lynx rufus.* Kenneth L. Duke, *Duke University, Durham.*

29. A captive skunk produces two litters in one season. Albert R. Shadle, *University of Buffalo, Buffalo.*

10:00 A.M.

Final Business Meeting

1:00 P.M.

Conducted tour of the Museum

2:00 P.M.

30. Embryo resorption and placental scar formation. Clinton Conaway, *University of Wisconsin, Madison.*
31. The electrocardiograph of the hibernating Arctic ground squirrel. X. J. Musacchia, St. Louis University, and Roland M. Nardone, *Catholic University, Washington, D. C.*
32. Changes with wear in the occlusal pattern in the upper molars of *Cuniculus paca.* Stuart O. Landry, Jr., *University of California, Berkeley.*
33. Variation in the fox squirrel in Florida. Joseph C. Moore, *Everglades National Park.*
34. The status of the name *Sciurus niger cinereus* Linnaeus and *Sciurus niger vulpinus* Schreber. Fred S. Barkalow, Jr., *North Carolina State College, Raleigh.*
35. The relationships of the early groups of Carnivora. Loris S. Russell, *National Museum of Canada, Ottawa.*
36. The California grizzly. Tracy I. Storer and Lloyd P. Tevis, Jr., *University of California, Davis.*

FRIDAY, JUNE 19

10:00 A.M.

Field Trip to New York Zoological Gardens (John Tee-Van)

DIRECTORS MEETING

The meeting of the Board of Directors was called to order by President William J. Hamilton, Jr. Harold E. Anthony was reelected as a Trustee to succeed himself for another three years. W. Robert Eadie was reappointed Editor. The reports of the Treasurer, Auditing Committee, and Trustees were read and accepted. In an attempt to reduce the excessively large list of delinquents, it was decided that members would be billed for annual dues in November and would be considered as in arrears after December 1. Budgetary allotments were made for the year and the Society's memberships in the American Institute of Biological Sciences and the International Union for the Protection of Nature were dropped. Financial support for the Zoological Record Fund was voted upon affirmatively.

The following budget was authorized for 1953:

Expenses of Treasurer	$ 450.00
Expenses of Corresponding Secretary	450.00
Journal of Mammalogy and Editor	8500.00
Honoraria for Young Mammalogists	200.00
Membership Committee	25.00
Contingent Fund	250.00
Zoological Record Fund	100.00

ANNUAL BUSINESS MEETING

The first annual business meeting on June 17 was attended by 52 members. Reports of the Corresponding Secretary, Treasurer, and Auditors were presented. The following officers were elected: William H. Burt, *President*; Robert T. Orr and George H. H. Tate, *Vice-Presidents*; Randolph L. Peterson, *Recording Secretary*; Keith R. Kelson, *Corresponding Secretary*; Caroline A. Heppenstall, *Treasurer*. Directors for the term 1953-1955 were elected as follows: W. B. Davis, J. Kenneth Doutt, Emmet T. Hooper, Colin C. Sanborn,

Viola S. Schantz. Oliver P. Pearson and Antoon de Vos were elected to fill the unexpired 1952–1954 terms vacated by Robert T. Orr and George H. H. Tate.

With deep regret the Society learned of the deaths of nine members, two of them Charter Members (*), in 1951: Elsie P. Anderson, Earle A. Brooks, Herbert L. Dozier, Charles W. Goodrum, Henry C. Hahn, Jr., *James L. Peters, Javier Ortiz de la Puente, *Clark P. Streator, Harry J. La Due.

As of the close of the year 1952 the Society had continued to grow in all respects although in some respects at a lesser rate than in 1951. There were 138 nominees for memberships, 13 resignations, 9 deaths reported, and 57 members dropped for delinquency in dues for three years. New subscriptions numbered 48, but 32 subscribers cancelled. The most significant gain was in the highly important category of Life Members; some 13 persons, including 1 nominee, began life memberships.

The Corresponding Secretary submitted the following summary of memberships, subscriptions, and mailing for the year ending December 31, 1952.

	1951		1952	
MEMBERSHIP				
Changes since preceding annual report				
Nominees		143		138
Resignations	29		13	
Deaths reported	5		9	
Members dropped (delinquent)	59		57	
Total		93		79
Net change		+50		+59
Status as of December 31, 1952				
Honorary members	5		7	
Life members	50		63	
Annual members	1293		1337	
Total membership		1348		1407
SUBSCRIPTION				
Changes since preceding report				
New subscriptions	71		48	
Subscriptions cancelled	50		32	
Net change		+21		+16
Status as of December 31				
Total paid subscriptions		431		447
MAILING LIST				
Total membership	1348		1407	
Members not receiving Journal	130		149	
Total members receiving Journal		1218		1258
Total paid subscriptions		431		447
Total mailing list		1649		1705
Net change from preceding year		+67		+56

The reports of the following committees and representatives were by the Corresponding Secretary read and accepted: Bibliography (David H. Johnson); Economic Mammalogy (E. R. Hall); A. I. B. S. (David H. Johnson); A. A. A. S. (E. R. Hall).

The second session of the business meeting was convened June 18. Sixty-two persons were present. The reports of the following committees were read and accepted: Conservation of Land Mammals (Ralph S. Palmer); Marine Mammals (Robert T. Orr); Nomenclature (Colin C. Sanborn); Memberships (Albert R. Shadle); Editorial Committee (W. Robert Eadie); Index (Viola S. Schantz); Board of Directors (read by Randolph L. Peterson); Representative to the Natural Resources Council (Frederick S. Barkalow).

Following the report of the representative to the Natural Resources Council, considerable discussion ensued relative to that organization's proposal to seek annual grants from various organizations. No positive action was taken.

Invitations to have the Society meet at the University of Southern California, the University of Utah, and a suggestion that the Society meet at Rocky Mountain National Park were presented for voting. The voting showed a desire to meet at Rocky Mountain National Park. The time of the 1954 meeting was tentatively scheduled for the middle of June.

Antoon de Vos again urged the establishment of an Associate Membership. No action was taken on this proposal.

The following resolutions were presented by the Resolutions Committee and passed:
(I) *Whereas* the Government of the United States of America has seen fit to subject grants, fellowships, etc. to payment of an income tax, and
Whereas this tax materially reduces the funds which the recipient has for his purely scientific research and deprives him of full opportunity to complete his work, and
Whereas the average salary of most museum workers is under $5,000. a year, and
Whereas it is felt that this is a tax on the advancement and dissemination of scientific knowledge, and
Whereas this being so, it is a severe reflection on the understanding and comprehension of scientific research by our representatives responsible for the levying of such a tax, and
Whereas it is further felt that it is a backward step and hinders the welfare of these United States of America,
Therefore, be it resolved that we, the Members of the American Society of Mammalogists, assembled in New York City on 17 June, 1953, at our thirty-third annual meeting, respectfully request that steps be taken to correct this situation and that this tax be removed from all bona fide grants, scholarships, fellowships, etc., given for scientific research.
(II) *Be it hereby resolved* that the American Society of Mammalogists at its 33rd annual meeting strongly disapproves of the bounty on wolverine, passed by the Alaskan Territorial Legislature at its 21st Session, and fully concurs with the following statements made by Clarence Rhode, Executive Officer of the Alaska Game Commission, in a letter to Hon. Ernest Gruening, Governor of Alaska, dated March 24, 1953:
"Bounty payments are not the answer to wolverine problems, either on trap lines or where damage to property is involved.
"Wolverine are a rare and unique part of the fauna of Alaska and provide a small but important part of the Territory's annual crop of fur. Their pelt has become an interesting and highly desired trophy. Stateside zoological gardens are in continuous demand for live wolverine and could use Alaska's entire annual crop at $30 to $100 per animal.
"The population in the Territory is stabilized at a fairly low level and further reduction in wolverine numbers will require some protective measures under the Alaska Game Law, at least during seasons of unprime furs. Control of numbers is certainly not necessary, although specific animals may become local nuisances.
"Bounty payments are an unnecessary cost to the Territory which at present is contributing nothing to the management of its fur resources."
(III) *Resolved:* That the American Society of Mammalogists in session at its 33rd annual meeting at New York City, 17 June, 1953, tenders its sincere thanks and appreciation to the President, Trustees, Director, and Staff of the American Museum of Natural History, to the officers and staff of the New York Zoological Society, and to the members of the Local Committee on Arrangements, especially H. E. Anthony, G. H. H. Tate, and John Tee-Van, for their generous hospitality and effective efforts contributing to the success of its 33rd annual meeting, and for the enjoyment of all members and their families and friends in attendance at this meeting.

As new business, Emmet T. Hooper raised the question of methods of programming of papers for the annual meeting. Considerable discussion followed and it was the concensus of opinion that the Corresponding Secretary should have the greatest possible latitude in arranging the programs.

OBITUARY NOTICES

Clark P. Streator (1866 to 1952)

Clark P. Streator, a charter member of the American Society of Mammalogists, passed away on Friday, November 28, 1952, at Santa Cruz, California.

Mr. Streator was a native Ohioan, who became interested in wildlife at an early age. In 1883, at the age of 17, he went to California and opened a taxidermist shop in Santa Barbara. In 1887 he located at San Francisco, where he resided for a year and became acquainted with the scientists of the University of California and the museum staff there. Then going east to Rochester, New York, he worked at Ward's Natural Science Establishment, and later, through the sponsorship of Charles Cory, he became an employee of the Field Museum of Natural History, Chicago, Illinois. After that he was engaged by the American Museum of Natural History, in New York, to make an expedition to British Columbia, where he collected bird and mammal specimens for that museum.

From 1890 to 1899 inclusive, Mr. Streator collected 5,734 mammal specimens for the U. S. Biological Survey, now the Fish and Wildlife Service, U. S. Department of the Interior. These specimens were collected mostly in the following states: Arizona, California, Idaho, Nevada, New Mexico, Oregon, Texas and Washington, and in Alaska, British Columbia and Mexico. Many new races were described from these specimens and five were named for Mr. Streator: *Perodipus streatori* Merriam, Proc. Biol. Soc. Washington 9: 113, June 21, 1894; *Neotoma fuscipes streatori* Merriam, Proc. Biol. Soc. Washington 9: 124, July 2, 1894; *Sorex personatus streatori* Merriam, North Amer. Fauna 10: 62, December 31, 1895; *Putorius streatori* Merriam, North Amer. Fauna 11: 13, June 30, 1896; and *Peromyscus maniculatus streatori* Nelson and Goldman, Jour. Washington Acad. Sci. 21: 531, December 19, 1931.

Mr. Streator's interest in mammalogy continued throughout his life. In 1951, at the age of 85, he attended the annual meeting of the American Society of Mammalogists held at Yellowstone Park, Wyoming. He was also a well known ornithologist, and a member of the American Ornithologists' Union.

Mr. Streator was married to Ida Lehman. He and his family moved to Santa Cruz, California, in 1896, where for almost 40 years he maintained a transfer business. He is survived by two sons, Nelson and Albert, of Santa Cruz.

Funeral services were conducted at the Irvin M. Smith Chapel, Monday, December 1, with interment at Cypress Lawn Cemetery, Santa Cruz, California.—Viola S. Schantz, *Fish and Wildlife Service, U. S. Department of the Interior, Washington, D. C.*

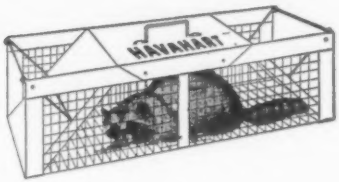
Sergey Ivanovich Ognev

"Sergey Ivanovich Ognev died on 20 December 1951 aged sixty-five. As a biologist he was especially interested in arctic mammals and wrote *Mlekopitayushchiye severovostochnoy Sibiri* (Mammals of northeastern Siberia) (Vladivostock, 1926). He also prepared an important systematic study, entitled *Zveri SSSR i prilezhashchikh stran* (Animals of the U. S. S. R. and adjacent countries), which includes the taxonomy and distribution of mammals of the Soviet Arctic."—From *The Polar Record, 6(45): 701, 1953.*

DATE OF ISSUE OF PREVIOUS NUMBERS

(*Correction*) Journal of Mammalogy, Vol. 34, No. 1, was mailed **February 19, 1953**
Journal of Mammalogy, Vol. 34, No. 2, was mailed **May 14, 1953**

HAVAHART HUMANE ANIMAL TRAPS



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SUGGESTIONS TO AUTHORS

The *Journal of Mammalogy* publishes original papers with significant new content on any phase of the science of mammalogy. While authors need not necessarily be members of the society, it is suggested that individuals publishing serious papers in this field should consider carefully the desirability of associating themselves with the American Society of Mammalogists.

Papers are generally published in order of receipt with some exceptions at the discretion of the editor. Papers over twenty printed pages in length are rarely published because of costs and limitations of space. When partly subsidized, such papers may occasionally be published at the discretion of the editorial committee.

Photographic illustrations (half-tones) and tabular matter are strictly limited because of high costs of printing. Half-tones for decorative purposes, or interest only, will not be published; they should illustrate some point or fact, best shown in this way, and essential to the exposition of the paper. Tabular matter should contain data not repeated in text.

1. All manuscripts should be typewritten on white bond paper (8½″ × 11″ or 8″ × 10½″) with *all material, including titles, quotations, and literature cited, double spaced*. All margins should be at least one and one-half inches wide and pages should be numbered at the upper right corner. Carbon copies will not be accepted, nor will originals on onion-skin paper.

2. Titles are best if short as an aid to bibliography. Ten words should ordinarily be a maximum and less will usually serve.

3. Acknowledgments are included in the text; footnotes are avoided. Note the position for authors' names at the beginning and authors' addresses at the end of the article.

4. The bibliographic style used in recent Journal issues should be noted carefully and followed in "Literature Cited." In general, the bibliographic style will follow the suggestions made in the report of the A. I. B. S. Publications Committee, the A. I. B. S. Bul., 2 (2): 21–23. Fewer than six references should be inserted in parentheses in the text, giving author, publication, volume, paging, and year, but not title unless a book. See recent issues for style.

5. Tabular matter should be arranged as simply as possible to fit Journal page size. Note style and place for title of table in recent issues. It is not always necessary to present all data gathered. The author should exercise some judgment as to what data are essential or of general interest. Tables should be typed on separate sheets at the end of the paper and *should not be placed in the running text*.

6. Line drawings or graphs should not be made on excessively large sheets. While some reduction is desirable, an original drawing or graph twice the size of the intended cut is ample. Photographic copies of drawings or graphs may not reproduce as well as the original. The original is preferred by the editor. Large sheets are cumbersome to handle and ship, and increase postage costs. Labels must be planned to be easily legible when reduced. Lines must be solid black, not gray, to reproduce well. Graphs on cross section paper should be made on paper with pale blue lines.

7. Photographs for reproduction should be sharp, with high contrast, and printed on glossy paper. A size of 4″ x 5″ is ordinarily most easy to arrange. The editor prefers them unmounted. Each should be identified by a notation on the back, lightly in pencil. Legends should be typed as paragraphs, in sequence, on a separate sheet at the end of the article. It is often possible to crop photographs extensively to remove non-essential areas such as sky, foreground, background, etc.

8. A brief, concise, and informative summary is advisable at the end of the paper.

9. Proof should be read very carefully immediately upon receipt and returned promptly, with manuscript, to the editor. While errors should be corrected, the galley proof is not the place for editorial changes by the author. Necessary changes are best at the end of a paragraph, or as a new paragraph.

10. Arrangements for reprints are *made by the author with the publisher* at time of receipt of proof. A form is supplied for ordering personal or institutional supplies of reprints. Fifty reprints, without covers, are supplied, free to the author of a major article. These may be obtained only if the author orders enough to bring the total number of reprints to 100.